

A CONTRIBUTION TO THE THEORY OF THE LIVING ORGANISM

BY

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MELBOURNE UNIVERSITY PRESS
in association with
OXFORD UNIVERSITY PRESS
MELBOURNE AND LONDON
1943

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ORGANISM

MELBOURNE UNIVERSITY PRESS
CARLTON, N.S. VICTORIA
in association with
OXFORD UNIVERSITY PRESS
MELBOURNE AND LONDON

NEW YORK: G. E. STECHERT & CO., 31 EAST 10th ST.

*Registered at the General Post Office, Melbourne, for
transmission by post as a book*

Wholly set up and printed in Australia by
BROWN, PRIOR, ANDERSON PTY. LTD.,
430 Little Bourke Street, Melbourne

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CHAPTER I

INTRODUCTORY

1. *The living organism as subject*

THE MAIN thesis of this book is that all living organisms are subjects; that all but the simplest organisms (and possibly even these also) are organizations or nexus of subjects; that the characteristic activity of a subject is the act of perception; and that perception is the establishment by the subject of its causal relation with its external world. Although I am not aware of any previous attempt to combine these propositions as a basis for an interpretation of the living organism, no originality is, of course, claimed for any one of them. The developments of biology and psychology are, however, continually providing a firmer factual and theoretical basis for their discussion, and Whitehead's *Philosophy of Organism* is specially adapted to deal with the philosophical problems involved in the thesis as a whole.

An outline of this conception of the living organism will be given in the present section. It will be the task of later chapters to elaborate and attempt to justify it, and to follow up some of its implications.

A living organism presents in its most complex form the problem so prominent in philosophical science, the problem of the unity or wholeness of a thing which is composed of separable parts. This unity can manifest itself in two ways. The first is that the whole acts as a *causal unit*. In this sense a living organism is a unity, and so also is a chemical molecule. Action as a causal unit means that the action of the whole is not merely the sum of the action of its parts. If a brick is thrown into water, it will cause a splash. If two bricks are cemented together, and the mass thrown into water, it will cause a bigger splash. There is, however, no important distinction between the action of the two attached bricks considered as a unit and the sum of the actions of the two bricks considered as separate units. The combined mass does not do anything that either part cannot do alone; it merely does the sum of what each part can do separately. A molecule of water, however, acts in a way which is not merely the sum of the activities of two atoms of hydrogen and one of oxygen. It acts differently from either, or from the sum of its constituents; it is a real causal unit, not three

causal units adding their effects together. In Whitehead's¹ terminology, both a molecule and a living organism are examples of a 'nexus,'² or organization of parts dependent on the mutual action of the parts on each other with the consequence that the whole acts as a causal unit both on its own parts and on other objects.

The idea of a multiplicity forming a unity can, however, be approached from another direction. In the unity of the self we have direct experience of such a unity. This is a unity of activity or process; and the constituents, or elements, of process are events. Happenings or events in widely distant parts of the body, in the eye and ear for instance, generate together the unitary experience of the recognition of a dangerous situation with the quality of fear and consequent appropriate action. The unity of the self is also a unity of temporally successive events. The character of the self at the moment is the outcome of the whole of its past experiences. The activities, or processes, of the living organism constitute, therefore, a nexus of events, the constituent events considered in isolation being both spatially and temporally separate.

In elucidating the nature of living organisms we shall be concerned primarily with the elucidation of processes, their analysis into events, and the mutual relations between the events by which they come to form wholes of a higher order. Structure is incidental to process. The structure of an animal or plant is the result of the process of embryonic development (morphogenesis) and makes possible other processes. Evolutionary change of structure is consequent to evolutionary change in the process of morphogenesis.

A living organism, at least any of the higher animals, is a subject which feels or experiences, and in which stimulus and response are connected by the mental act of perception. But such animals are composed of smaller living organisms, the most conspicuous of which are cells. These must also be regarded as feeling, perceiving, subjects. The justification for regarding its living parts as being, in this respect, of the same essential nature as the organism as a whole will be elaborated later. At the moment it is sufficient to refer to the fact that tissue culture technique has

1. A list of references is given at the end of the book.

2. The word is taken from Whitehead, who uses the Latin form of the plural, *nexus*. Throughout this book, however, I shall use it as a completely anglicized word, with a plural of same form as the singular.

shown that isolated cells or groups of cells can maintain life apart from the body from which they were taken; that the cells of the adult are the direct descendants of, and therefore cannot be fundamentally different from, embryonic cells, the behaviour of which as percipients is discussed in chapter v; and that they have the general character of such free-living organisms as the amoeba, the behaviour of which is discussed in chapter iv.

The propriety of introducing their subjective experience into the interpretation of the activities of all living organisms is of course denied by many biologists, and for various reasons. This question will be discussed in relation to some special problems as they arise. As a matter of scientific method, however, the justification of this mode of procedure must be the same as that of all scientific concepts; for instance, those of the atomic structure of matter and energy. These are justified by their success as explanatory systems, meaning by explanation the formulation of general principles of which apparently diverse phenomena can be shown to be special instances.

In all animals which are themselves subjects, one problem of their unity is therefore the problem of how a multiplicity of subjects can combine to make a subject of a higher order which both transcends and includes them. Indeed if, as we must conclude,³ the component subjects precede in embryonic development the subject which is the organism as a whole, that subject not only includes the component subjects but is, in a sense to be discussed, generated out of them, in a manner analogous to the generation of a molecule by combination of previously separate atoms.

Although all multicellular organisms are nexus of subjects, not every such organism, taken as a whole, can be held to have the special form of unity of being itself a subject of higher order. Observation of their behaviour does not support the idea that a tree or a sponge behaves as a whole as a percipient subject. The unity of such organisms depends on a continuity of substance (or partial continuity through semi-permeable membranes) which carries a 'biological field' (chapter ii). The unifying action of the field is to be conceived as producing a community of action of the cells or other living parts which collectively constitute the carrier of the field and which respond to the conditions provided by the field. Biological fields are, of course, also present in organisms which have the higher grade of unity of a subject. This will be

3. For reasons given in chapters ii and v.

discussed later, especially in relation to the morphogenetic fields of the developing embryo. Two grades of unity in living organisms have therefore to be studied. There is the lower grade of unity brought about by community of action of a multitude of subjects, and also the higher grade of unity achieved when the constituent subjects not only act in this way, but also give rise to a subject of higher order through which their activities are more intimately co-ordinated to give the responses to stimuli on the part of the organism as a whole. Among organisms exhibiting the unity of a subject we must, I think, include all animals from worms upwards, if not indeed all animals except perhaps sponges; though with varying degrees of independence of the subsidiary subjects.

So far, I have spoken of the component, subsidiary subjects as the cells. The concept of the cell presents, however, some difficulty. It is no longer possible to maintain in its original simplicity the notion which was embodied in the old 'Cell Theory,' that the body of an animal is built up of cells which are easily definable units, each consisting of a nucleus with surrounding protoplasm and delimited from its neighbours by a partition (the cell membrane). In many tissues this is the case, though often protoplasmic continuity between the cells is maintained by connections passing through the membranes. Even where these do not exist, there is a partial chemical continuity by passage of diffusible substances through the membranes. In other tissues and organs, however, no cell partitions can be seen; they consist of a mass of protoplasm containing numerous nuclei. Moreover, some Protozoa are cells in the strict sense defined above, and others have several nuclei and yet are certainly 'units' in the same sense as otherwise closely similar forms containing only one nucleus.

Nevertheless, the cell can in an important sense be considered as the living unit of structure of a higher animal or plant, although the precision with which it can be delimited from its neighbours varies in different cases. The cell, defined anatomically as a small mass of protoplasm containing a nucleus and bounded by a cell membrane, is the most simply organized anatomical part that is capable of continued life when separated from the organism of which it formed a part. Whatever its relation to the rest of the organism while it formed a part of that organism, when separated from it artificially, or naturally as in the case of blood cells or germ cells, it delimits itself from its environment by a cell

membrane if one was not already present, and leads the life of a self-contained organism.

We shall therefore continue to speak of cells as the living units of structure of the body, in spite of the fact—implicit in the idea of the organism as a whole—that so long as they are parts of the whole, their organic continuity with the neighbouring units is as characteristic as their actual or potential separateness from them.

A multicellular animal is, however, not merely an organization of cells, however these are defined. It is a hierarchy of organizations of increasing inclusiveness. These organizations, intermediate between cells and the animal as a whole, are organs, tissues, and so forth, often of great complexity. In the nervous system for instance, which is one of the most important of these intermediate organizations, the cells (neurones) are organized into nexus of increasing complexity and inclusiveness, beginning with the simplest reflex arcs, then the spinal cord centres, the integrated spinal centres correlated with the limbs, the spinal cord as a whole, the various co-ordinating centres in the brain, and finally, in the higher animals, the cerebral cortex. These nexus are in most cases marked out by recognizable anatomical arrangements. In others, they appear to come into being as temporary functional units.

The argument of this book will be based on the premise that cells are subjects, and that the animal as a whole is a subject. It will not be necessary for our purposes to come to any decision as to whether the intermediate organizations of cells, such as organs or tissues, have or have not, as wholes, the status of subjects, though this question will receive some attention in chapter v in regard to the regions carrying morphogenetic fields in the embryo. They have indeed the form of unity I have described as acting as a causal unit. I will therefore introduce the word 'agent' to express a region or nexus of activity, acting causally as a unit. An agent may or may not also be a subject. In the case of the animal as a whole, or of a cell, the agent is itself a subject. An agent such as a muscle, being a nexus of cells, is a nexus of subjects, but it does not seem necessary to assume that it is, as a whole, a subject of higher order. A cell, though a subject, must probably also be considered a nexus of living sub-agents. Apart from such general features as cytoplasm and chromosomes, such parts as cilia, for instance, appear to have the same type of relation to the cell as a whole as the cells or organs of multicellular animals

have to the animal as a whole. I believe it follows, if the general argument to be developed in this book is accepted, that these living parts of a cell are also subjects, and that therefore the cell is a subject constituted out of subsidiary subjects. It is, however, not necessary at present to take up any definite opinion as to the subject status of the living parts of a cell.⁴

Living agents may therefore be elementary subjects; for instance, cells, or if these are considered as nexus of subjects, the sub-agents of the cell. Or they may be nexus of subjects, whose unity of action is due to similar environment provided by the biological field of which they form a part. Or they may be constituted of a nexus of subjects which in combination give rise to a subject of higher order. When an agent is constituted in this way, I shall speak of the subject of higher order as the *central agent*. The most conspicuous example of a central agent is the one which is concerned with the behaviour of the animal as a whole; that is to say, its behaviour considered as a subject and not merely as a nexus of subjects. If a cell is to be considered, not only as a subject but also as a nexus of component subjects, the subject which is the cell as a whole is the central agent of the cell, having the same relation to its differentiated living parts as the central agent of the animal as a whole has to its component subjects.

A central agent might therefore with equal propriety be termed a central subject. The former term seems preferable however, for the term 'agent' must be retained to describe a nexus of subjects, or indeed any nexus of activity, acting as a causal unit without implying either that it has or has not, as a whole, also the unity of a subject. To use the term 'central subject' while retaining the term 'central agent' for the other type of nexus would suggest that an agent is always to be contrasted with a subject. Since, however, every living agent, if not itself a subject is at least a nexus of subjects, it is often less important for the purposes of our argument to decide whether or not it must be considered itself a subject than to realize that it is composed of subjects.

Moreover, the word 'agent,' even when that agent is a subject, is useful as including not only its activity as a subject, but also its anatomical aspect.

The locus of the Central Agent⁵ concerned with the behaviour of the animal as a whole is the brain, especially the cortex in the

4. The relation between 'living' and 'non-living' will receive attention in chapter III.

5. For convenience I shall in future refer to the central agent which is concerned with the behaviour of the organism as a whole as 'the Central Agent' with capital initial letters.

higher animals. This is its locus in the sense that the vital processes of the neurones in the brain provide the immediate psychophysical field⁶ for this agent. But as these vital processes are in continuity with the vital processes of the peripheral nervous system, and through them with those of the body as a whole, its locus can only be thus delimited as a matter of convenience. Like all the other agents of the body, the Central Agent is a nexus of processes, and the spatial boundaries of this nexus cannot be sharply defined from the surrounding processes with which it interacts, nor are they even necessarily constant, still less bound up with any anatomical structure. Indeed, to ascribe a spatial boundary to any nexus of processes is a matter of convenience only, for it is necessarily in causal relation to other contiguous processes. This applies also to a magnet or a chemical atom.

As already stated, the characteristic activity of a subject is the act of perception. This will be discussed more fully in chapter III, where we shall also take into account the fact that the organism is not merely a subject but a nexus of subjects. A preliminary consideration of the nature of perception, so far as it concerns our argument is, however, necessary at this point.

In recent years there has been a tendency to stress the conative aspect of perception rather than its purely cognitive side. In accordance with this variation of stress we find at one end of the scale such a definition of perception as an act of the mind by which it refers its sensations to an external object as their cause. At the other extreme is the bodily adjustment theory of perception. According to this theory, to perceive an object as a wheel-barrow rather than as a dog is to adjust our muscular system to appropriate action. The object is to us a wheel-barrow because of the incipient tension of the muscles appropriate to handling it. Price thus characterizes the bodily adjustment theory of perception (p. 156): 'There is the sensing of the sense-datum (which really is a form of consciousness and an intuitive one), but over and above that, there is only the automatic adjustment of our body in a certain way.'

Both these extreme definitions, however, ignore essential features of perception. We shall take it that all perception involves cognition, conation, and affective tone. Too exclusive attention to advanced forms of human visual perception has tended in the past to over-emphasize its cognitive aspect. While the bodily

6. See chapter II.

adjustment theory goes too far in the opposite direction in maintaining that there is nothing essential in perception beyond the sensation and the motor adjustment, the theory has served to stress the fact that, primitively, objects are perceived dominantly in terms of action, or possible action, appropriate to them. To a child, and indeed, except under special circumstances, to an adult also, a chair is something to sit on, an orange is a particular kind of edible object. We may confidently assume that to a rabbit the difference in meaning between the sight of a dog and the sight of another rabbit is primarily a difference of appropriate action.

The response which is implicit in perception need not necessarily follow as overt action, but appropriate possible action is an essential part of the meaning of the sensum.⁷ We perceive an angry dog primarily as something to be avoided. 'When I recognize an object as a tree a rudimentary conation is involved, since the recognition implies a latent readiness to react appropriately to it, mentally or physically. The primary reason why both ash and elm are regarded as trees is that the same reactions will serve for each and they only become differentiated when specific needs arise.' (Wolters, p. 137.)

A definition of the act of perception, which is not an exhaustive definition but which defines its characteristic which is of principal importance for our purposes, may be given as follows: An act of perception is the establishment by the subject of its causal relation with its external world at that moment.

It is maintained that this interpretation of the nature—or perhaps, the function—of perception is not an inference but is given in the experience of perceiving. This is fundamental to Whitehead's system (chapter III). Meanwhile we may refer to Whiteley's paper on the 'Causal Theory of Perception.' This theory states that sensa are caused by physical objects in the external world. One well-known philosophical objection to this theory is that since we can only know these physical objects by the sensa they cause in us, the assumption of a physical object as the cause of the sensum adds nothing to our knowledge. According to Whiteley, objections to the causal theory of perception are due to the false conception that sensing is a purely cognitive process. Actually, however, sensing is not a kind of knowing but a kind

7. The choice of one out of the group of words—sensation, sense-datum, sensum, presentation, etc.—meets with the difficulty that special theories of the nature and status of these objects of experience are associated with all of them. No implications as to the nature of sensa are intended by the choice of this word, beyond those which will be developed in chapter III.

of feeling; a feeling of something acting upon us. Perceiving is the activity of the subject both as patient and agent in a causal process. The subject's awareness of himself as patient only, as effect and not as cause, would be 'pure sensing'—for example, the awareness of redness, without a trace of 'meaning' in the experience. Purposes⁸ are the subject's awareness that he is not merely an effect but also a cause. The affective tone of an act of perception in which a sensum acquires the meaning of avoidance, is fear; the affective tone of the perception of an object as one towards which sexual action is appropriate is sexual emotion.

The feeling of something acting upon us is much less prominent in the experiencing of visual and auditory than of tactile sensa. Nevertheless, our discussions of perception will deal mainly with visual perception, for this is the form of perception most amenable to analysis. As in so many other vital functions, we can learn more about them by study of their more specialized than of their more generalized manifestations.

If perception is the establishment of the causal relation between the subject and its external world, it follows that it has an anticipatory character. Any response to a stimulus (experienced as a sensum), if it is to be appropriate, must be appropriate not to the present situation but to an anticipated future situation. Even the avoidance response to a painful stimulus is a response appropriate not to the present feeling of pain but to an anticipation of a continuance of the pain, or of future relief from the pain. The most primitive form of perception, devoid of all modification by experience, consists in the relating of the sensum to one of the percipient's potential modes of behaviour. This word, rather than movement, is used designedly, to imply that it is movement or action directed towards a goal. A rabbit's flight from a dog is not merely the physical effect of the visual stimulus, like the motion of a wound-up clock-work mechanism when the release is withdrawn. The element of anticipation in the action is shown by the fact that the rabbit seeks for cover as it runs; it does not merely come to rest if it happens to run into cover. A small element of prior experience no doubt enters into this behaviour, in that the rabbit has already had experience of the different affective tones of the situations, being in cover and being in the open, though not in relation to the particular situation of its first

8. In the percipient act itself, the term 'subjective aim' is more appropriate than purpose. See chapter III.

perception of a dangerous object when it is in the open. As will be argued later, however, anticipation or goal-seeking must be postulated in many cases of the first performance of an instinctive action totally devoid of all relevant prior experience.⁹

Price has emphasized the prospective or forward-looking character of human perception, in which, of course, the anticipations inherent in the act of perception have, by the time a man arrives at self-consciousness, been rendered detailed and precise by previous experience. Price says: 'For it is what we may call the developmental aspect of the material thing, its "tendentiousness," that we chiefly attend to in the perceptual act. It presents itself to our mind not just as being so and so, but as about to become or to do so and so—as about to jump or to fall or to strike' (p. 161). Or what it is about to do may be just to go on as it was before; this not-likely-to-move character may be the main character that strikes us in such an object as a rock. Indeed the idea of a material object is dependent upon this anticipatory character of perception. To a human percipient the visual sensum correlated with a tree is a patch of green of a certain shape. This, however, carries with it the anticipation of other sensa obtainable from the same source, such as hardness, the feeling of climbing into its branches, and so on, including changes in the visual sensum itself as we change our position in respect to the tree. In fact, the visual sensum implies all the other properties of the tree which can be known through the senses. 'Every perceptual act *anticipates its own confirmation* by subsequent acts' (Price, p. 179); this is brought about by the building up of a 'family of sense-data.' We interpret a certain visual sensum as a tree because we are confident that under appropriate conditions we should experience all the other sense-data of the family.

It follows from this account of perception that the meanings given to sensa are the anticipations inherent in the act of perceiving, and that affective tone is the quality of the anticipations. The only affective tones in the most primitive types of perception are probably those of acceptance and avoidance. With increasing complexity and differentiation of receptor and effector organs (and consequently of perceivable objects) these become differentiated into hunger, fear, sexual emotion, and so on.

It must not be taken that the use of the word anticipation in

9. Perhaps the nearest we can get to a purely instinctive experience is the feeling of irrational fears; for instance, seeing a ghost, with its undefined but horrifying anticipations.

perception implies a consciously formulated anticipation. The problem of consciousness in perceiving is discussed in chapter III. We may point out at once, however, that our own perceptions involve anticipations which are certainly not consciously defined; they are only revealed by our surprise when they are not fulfilled. If I touched a table and it offered no resistance to my hand, my surprise would reveal that my visual perception of the table included the anticipation that it would be found to have the other properties common to tables.

Using the conception of a family of sensa-data (or sensa, as we shall call them) it is clear that the more specific and elaborate the family, the fuller is our cognition of the object. The external world of the lowest organisms, which are incapable of experiencing well-defined different kinds of sensa, cannot contain discrete objects of the kind we know. The discrimination of objects, for which the sense of sight is specially effective, is the breaking up of the causal relation between the subject and its external world into separate components, the action of which on the subject can be discriminated from the total causal action of its external world, and on which the subject's own actions can be directed. This power of discrimination depends upon specialized sense organs, and would be useless without concomitant differentiation of effector organs. Indeed, if our definition of perception is correct, it would be impossible without this differentiation, for by our definition objects become differentiated not only because they act differently on the subject, but also because the subject can act back differently on them. Perception can only be in terms of a situation as a whole in the case of organisms incapable of breaking up the total causal relation between itself and its external world into components (objects). We must assume also that to animals intermediate in position between these lowest organisms and man, their external world is peopled by objects of a kind different from those which we know. An animal which has little power of learning by experience, and which therefore has little power of building up new families of sense-data, and whose actions are therefore mainly instinctive, can presumably only analyze its causal relation with its external world into a few components. Its world would contain only a few classes of objects, such as edible and not edible, avoidable and acceptable, sexual and not sexual. With increasing powers of sensory discrimination and of learning by experience, and with increasing versatility of effector organs,

the number of kinds of objects increases. No one watching a monkey examining and pulling things to pieces could doubt that its world contains a much greater variety of objects than does the world of a horse.

The definition of perception as the establishment by the subject of its causal relation with its external world makes it necessary to use the word *sensum* with a very wide meaning, or else to recognize that other objects of experience can function like *sensa* in the subject's awareness of the causal action of its external world upon it. In its narrow meaning, a *sensum* is the effect on the Central Agent of processes in the sense organs, transmitted to it by the intermediation of nerves. Such feelings as those of fatigue, the feelings of bodily movements, and vaguer feelings of comfort or discomfort, must also be included in the category of *sensa*. All these, originating in the body, are part of the external world of the Central Agent. We shall have to go further than this, however, and accept Whitehead's view that we experience our immediate past in essentially the same way as we experience *sensa*. Whitehead calls this 'non-sensuous perception.' This conception will also be elaborated in chapter III.

We have stated that in elucidating the nature of living organisms we shall be concerned primarily with the elucidation of processes. The elements we find by analysing process are events. Analysis of physical process leads to such elementary events as electronic vibrations and light waves. Acts of perception are elementary mental events. The relation between physical and mental will be discussed later; in the meantime we may give the name 'vital events' to all events characterizing the living organism as such, in contrast to constituent events of a lower order such as molecular events. Every vital event involves a mental event, the type of which is the act of perception. The distinction between vital events and events of a different (or 'physical') order can be clarified by the following illustration. If a *Paramecium* swimming in a drop of water be kept under observation while the temperature of the water is gradually raised, the velocity of its movements will be seen to increase, but up to a point they will not alter in character. As the temperature continues to rise, however, there comes a point where the movements change their character. Before this point, the animal was moving for a short distance in one direction, then turning and moving off in another, like fish swim-

ming about 'aimlessly' in a pond. The new type of movement is different and very characteristic. The Paramecium darts off in one direction, but after a short distance reverses its motion, darts backwards, and then may swing round several times in a circling movement. Jennings, who has analysed this part of the behaviour in detail, has shown that it has the function of testing the quality of the surrounding water. Then perhaps it rushes in short zig-zags across the whole width of the drop, and again starts its alternating short dashes and circlings. In fact, its behaviour is such that if it were a larger and more familiar animal we should say that it was frightened and seeking a way of escape.

Below the temperature at which the change in the type of movement took place, which is at about the point where the heat if continued would become injurious to the animal, the change in the velocity of the movement is not a vital event. Doubtless the cilia beat more quickly with rising temperature because the velocity of the chemical reactions concerned increases with increasing temperature. The change of velocity of the Paramecium as a whole is directly attributable to the change of velocity of chemical processes taking place within the organism, and does not concern the living organism as such. If there should happen to be dissolved in the water any chemical substances reacting with each other, this reaction would be speeded up similarly.

The change in the action which takes place when the temperature reaches a point which is critical for the Paramecium is of a different type. It is to be interpreted as the consequence of a vital event. The heat stimulus at this point evokes an act of perception. The changes produced by the rising temperature on the physico-chemical processes in the Paramecium (or in its surface layer if this is considered as a receptor-organ) are experienced as a sensum, an experience which carries with it the anticipation of further experience and action relevant thereto (the 'meaning' of the sensum). Naturally no well-defined intellectual content must be attributed to the anticipation. It may be conceived rather as an anticipatory feeling of continuing experience. The action is relevant in that it is appropriate for escape from the dangerous area, if this is possible.

Although the view of the living organism expounded in this book is the antithesis of a mechanistic theory, nevertheless it must be recognized that all energy transformations in the body which

result in work being done are due to mechanisms comparable *in this respect* to humanly constructed machines.

‘. . . we must be very careful not to let our physical or physiological concept of mechanism be narrowed to an interpretation of the term derived from the delicate and complicated contrivances of human skill. From the physical point of view, we understand by a “mechanism” whatsoever checks or controls, and guides into determinate paths, the workings of energy; in other words, whatsoever leads in the degradation of energy to its manifestation in some determinate form of *work*, at a stage short of that ultimate degradation which lapses in uniformly diffused heat.’ (Thompson, p. 161.)

Mechanisms may therefore be on the gross anatomical scale, or they may be of molecular dimensions such as those which bring about the polarity of a cell in mitosis. Everything that an organism *does*, from local concentration of chemical substances to the most complicated behaviour, depends upon mechanisms in this sense. Although however in relation to the organism as a whole these are its effector mechanisms, considered in themselves they may be living organisms, employing sub-mechanisms of their own.

As perception always carries with it the anticipation of further relevant experience, and the meaning of the present experience includes action, or potential action, appropriate to the anticipation, the notion of final causation is involved. This, and its relation to efficient causation, will form an important part of later discussions. At present, we may point out that the anticipatory aspect of perception compels us to recognize the reality of final causation in all perceiving organisms. Anticipation implies the potentiality of directing action in accordance with that anticipation; otherwise it would have no function. Without that potentiality an anticipation would be a mere useless prevision, and a very fallible prevision at that. It is true, of course, that we can anticipate an occurrence such as an eclipse of the moon, which we cannot influence; and that one may anticipate a disagreeable experience which one is powerless to avoid. This, however, only shows that there are limits to our power of influencing the future, and does not destroy the argument that the function of the capacity of anticipating future occurrences is to influence present action in relation to that anticipation. Causation in this sense is teleological or final causation. It is directed towards bringing about a situation which is not yet existent. The fact that other occurrences may

prevent the actualization of this situation merely emphasizes the justification of linking anticipation with causation. If a situation, anticipated or purposed by the subject, always occurred as anticipated, the anticipation would again be merely prevision, and there would be no point in ascribing causal action to the subject.

To ascribe perception, and therefore final causation and purpose, not only to all independent living organisms but also to embryonic and tissue cells, is to lay oneself open to the charge of confusing science with philosophy. It may be maintained that even if final causation is a real factor, science is not concerned with it, for it is not measurable, nor is it amenable to experiment. For instance, Needham maintains that this attitude is the only admissible scientific methodology, though not to be considered a metaphysical doctrine, and therefore not to be confused with materialism. He calls this standpoint neo-mechanism. According to Needham, all science is concerned only with what is measurable, and it is impossible to measure final cause. Hence biology is only science so long as it is biochemistry and biophysics. Psychology cannot be considered a science, because of its qualitative and non-mathematical character.

This seems, however, an altogether arbitrary limitation of the content of science, and would involve the coining of a new word for the study of living organisms as concrete objects without abstracting from either their physical or psychical features. A biologist, unless he takes the position that he is radically unique among living organisms, is concerned with experiencing subjects whether they be his fellow men, lower animals, tissue cells or even simpler organisms. Therefore it is not only legitimate but, as we shall maintain, necessary, for him to include in his explanatory schemes factors which are unnecessary for the explanatory schemes of the physicist—namely, such concepts as memory, anticipation, purpose, final causation—in a word, perception. Of course there is danger of an improper use of these concepts, and a large part of this work will consist of an attempt to define their proper use.

Another charge that is often brought against persons who introduce non-physical factors into their causal explanations of the actions of living organisms is that they are introducing 'mysterious' or 'mystical' elements to fill a gap in physical knowledge. The reply to this is: first, that it cannot be conceded that mental factors such as memory, anticipation and purpose, with which we have direct acquaintance, can be called mysterious, implying as it

does that physical concepts are, by comparison, intelligible; second, they should not, and need not, be used to fill a gap in physical knowledge. It may be possible in principle to describe every human response to a stimulus in terms of physical events in the body and brain, even when the response is connected with the stimulus by a long chain of reasoning. The chain of physical events intervening between stimulus and response could then be correctly exhibited as a chain of physical causation. We are maintaining, however, that mental factors enter into the structure of the chain of physical causation. One way in which this can be conceived is that which Whitehead has elaborated, and which will be discussed in chapter III.

I should perhaps state at this point that I have no intention of making use of the concept of purpose, or of Mind (as contrasted with minds) as a universal teleological principle, or God, ordering the course of nature to some future state as we guide our own consciously purposed acts to a conceived end. Purpose, as I shall use it, always characterizes the acts of agents (which in their dynamic aspects are nexus of events), and the purposive acts of agents are always directed to their own private ends. I regard it as essential to the proper use of the concept of purpose to identify the purposing agents. Whether the course of nature requires the assumption of a purposing agent embracing the whole of nature is, of course, a legitimate subject of inquiry, but, in spite of the severe limitation thus set upon the philosophical scope of this work, it will confine itself to the purposive acts of those agents which can be discovered by scientific methods. It will become obvious, also, that the mental processes which we shall be concerned with are limited to those closely concerned with sensory perception.

2. *Purposive action by living organisms*

The chief objective indication of purposiveness in the behaviour of living organisms is the familiar fact that the sequence of acts by which the goal is attained is not always the same. On different occasions the organism reaches the same end by different routes. (By the 'same' end is meant a 'functionally equivalent' end.) Even in the most rigidly instinctive behaviour the animal must always fit the details of its action to the special situation. The completed nest, the spider's web, the act of mating, is attained by a train of acts different in detail on every occasion. In embryonic develop-

ment this is also the case. The most conspicuous example of this is the development of a functional adult, or organ, after the experimental introduction of profound disturbance in the early stages of development. But this is only an extreme case. As every embryologist knows, the course of normal development varies in detail in embryos of the same species, as does the performance of an instinctive action.

In the sphere of behaviour this characteristic is exhibited as 'trial and error' when elements of complete novelty are present in the situation, and as 'insight' when it is a question of combining into a unitary action existing potentialities of response to elements in the situation which are not normally combined.

Many attempts have been made to eliminate the concept of purpose from the explanation of the fact that different routes may be followed to achieve the same end-result. Perhaps the favourite type of theory at present is one which accounts for the facts on the principle used in Gestalt psychology, namely, that certain physical systems tend to a state where the potential energy is at a minimum. It is easy to imagine, or construct, such physical systems which will reach the same end-state by intervening stages which differ according to differences in the initial configuration of the system. Further examination of the characteristics of responses to stimuli must be made before explanations of this type can be discussed. In the meantime it must be admitted that the causal efficacy of purpose cannot be *proved* in the sense that all other explanations are excluded. As Woodger says (p. 485), 'It is always possible to defend microscopic mechanism *in principle*, if anyone wishes to do so, by making your mechanism complicated enough, and by postulating enough sub-mechanisms to meet all contingencies. It *cannot* then be refuted, but neither can it be verified.' Anyone who accepts this explanation must, of course, accept it also for his own consciously purposed acts, unless he holds that factors enter into human behaviour which are different, not only in degree but in kind, from the factors determining the acts of lower organisms.

The fact that the activities of living organisms commonly have consequences beneficial to them cannot itself be used as an indication that they are purposive; nor can the fact that they occasionally have harmful consequences be taken as showing that they are not purposive. An animal which tries to satisfy its hunger with poisonous food is clearly acting as purposively as

one which satisfies it with wholesome food. The fact that the moth gets burnt is not relevant to whether its flight to the candle flame was purposive or mechanistic. The fact that most of the activities of animals have consequences beneficial to them is capable of explanation, in principle at any rate, on familiar Darwinian lines. Granted that organisms vary in regard to their innate modes of response to stimuli, and that these variations are inherited, then the principle of natural selection accounts for the evolution from a common ancestor of different types of organisms characterized by activities tending to their survival. But though natural selection may be invoked to explain how it comes about that the activities of organisms commonly have results beneficial to themselves and the species, the question whether these activities are purposive or not is more fundamental. In fact, what natural selection does in this respect is to preserve those organisms whose acts are purposed to ends which have more remote consequences favouring the survival of themselves and the species, and to eliminate those whose acts are purposed to ends having harmful consequences. The utility or harmfulness of the acts of organisms is therefore not itself relevant to the problem whether they are purposive or not.

Throughout this discussion I will use the word 'purposful' for an act directed towards an end or goal when that end is consciously conceived, and 'purposive' for an act directed towards an end when we have to leave undecided the question whether the end is consciously conceived or not. If our argument is correct, the responses of my tissue cells to stimuli are purposive acts, though I am not even aware that they are going on. But I am not the agent concerned in the response of my tissue cell. The agent is the cell itself, and if the ends to which its actions are directed are consciously conceived, they are conceived by the cell and not by me. We are not, however, concerned at present with the question whether or not an agent must be conscious of the ends to which it directs its actions.

Since a purposive act in the sense we are using it is always the act of an agent, the first task in considering whether an act is purposive or not is to identify the agent, and this brings us at once to a source of confusion in the use of the concept of purpose in biology.

It is common to distinguish between a reflex and an instinctive act on the grounds that the former is mechanistic, or at least not

purposive, while the instinctive act is purposive. The validity of this distinction, however, cannot be assessed without consideration of the agents which carry out the two actions. Let us consider the reflex act of blinking when a speck of dust falls on the cornea, and the instinctive action, culminating in mating, which is the expression of the sexual instinct. To say that the act of blinking is unpurposed, and the behaviour ending in mating is purposed, is to imply a comparison between incomparables. Analysed into its components, the reflex act is composed of a series of cell responses to stimuli—that is to say, the responses of a number of agents, the receptor neurone ending on the cornea, the motor neurone, the muscle cells, and perhaps others. To the external observer, the series of actions making up the blinking reflex has the useful result of protecting the cornea, and so preserving the power of vision; the series of actions culminating in mating has the useful result of continuing the species. But there is no agent that we know of which is purposing the preservation of the eye, nor the continuance of the species. Purpose has to be looked for in the living agents which carry out the actions. The man is not the agent concerned in the reflex blink, nor is the species the agent concerned in mating, though the interests of each are served by the actions.

In each case the purpose of the agent—whether it be the cells of the reflex arc or the animal under the sexual urge—is to act according to the meaning which the total situation has for it. This meaning is determined by the prehended stimulus (the sensum) and the character of the nexus of processes into which it is prehended. The latter gives the disposition¹⁰ of the agent. It has a disposition or tendency to respond in a specific way to a specific situation. The animal's response to the sexual object is the activity of mating. But its goal is solely to mate. It has no concern with the wider 'purpose' of ensuring the continuance of the species.

Consider again the agents in the reflex action—for example, the receptor neurone in the cornea. This may also be considered as having a disposition to act in a certain way in response to a specific stimulus—in this case the irritation of a speck of dust lying on the cornea. Here again, the cell is no more concerned with conserving the visual function of the eye than the mating animal was concerned with the continuance of the species. Its goal is a

10. See chapter III.

much more modest one. It is simply to act according to the meaning which the prehended stimulus (the sensum) has for it, which is to initiate a train of nerve impulses. Naturally none of the objective signs of purposiveness are to be observed in this act, for it is inaccessible to the necessary kind of observation. Moreover, even if it were accessible, it is doubtful if these signs would be forthcoming. For the extreme simplicity of the act gives little scope for variation in the method of accomplishing it, or necessity for indirect methods of achieving the goal. Consequently, whether or not we are to attribute purpose to the neurone in the same sense as we ascribe it to the mating animal will depend upon indirect considerations which will be developed later.

3. Instinctive and learnt behaviour

The dispositions of the perceiving agent which give specific meanings to the sensa produced by the speck of dust or the sexual object are instinctive dispositions, but dispositions of different agents. Owing to the various ways in which the terms 'instinct' and 'instinctive' have been used, it is necessary now to indicate the way they are used in this work. As all students of animal behaviour know, there has been much controversy about the proper way of distinguishing instinctive behaviour from reflex action on the one hand, or from learnt behaviour on the other hand—or indeed about the validity of any such distinction at all. As already indicated, we take the view that the distinction between instinctive behaviour and reflex action is a distinction between the agents concerned, not a distinction between different modes of behaviour. It remains therefore to differentiate between instinctive and learnt behaviour—or as the problem is often formulated, between instinct and intelligence, where intelligence is used in the restricted sense of capacity to learn by experience. As usual, however, precision of discussion is facilitated by using the adjectival rather than the substantive forms of the contrasted terms.

As so many writers have emphasized, it is often difficult or impossible to determine in any given instance of behaviour how far its course is determined by inherited factors, and is therefore instinctive, and how far it is determined by relevant past experience and is therefore learnt behaviour. Indeed this problem, like the problem of 'innate and acquired characters' in general, can only be discussed profitably if we concern ourselves, not with behaviour

or anatomical features as such, but with the source of the differences between observed instances of behaviour or anatomical characters.

The differences between the modes of feeding their young exhibited by birds and mammals is a difference of instinctive behaviour, in spite of the fact that the details of the actions of both may be, and almost certainly are, influenced by their past experiences. Differences in the behaviour of two sparrows searching for food for their young are no doubt due to differences in their previous experience of finding food, but the difference between the modes of feeding their young displayed by sparrows and rats is referable to different constitutions of the animals as they have developed by the process of embryonic and post-embryonic development. This again is traceable to differences in the constitution of the zygotes from which the sparrows and the rats developed.

With this use of the terms, the basis of all behaviour is instinctive; learnt behaviour is instinctive behaviour relevantly modified by past experience. Reflex action is here interpreted as instinctive behaviour of agents of a lower order than the Central Agent. It follows therefore that much of what is ordinarily spoken of as physiological processes is instinctive behaviour of lower-order agents. There is at present little or no reliable evidence that these agents can modify their behaviour relevantly to past experience, though, of course, the behaviour will run different courses in different environments. As is plain from the earlier discussions, instinctive behaviour, whether modified by experience or not, is regarded as purposive. The affective tone of achievement of the end is satisfaction.

Although it must be assumed that the goal to which purposive behaviour is directed is in some way represented in the present (since a future, non-existent, situation cannot be the cause of a present event running a particular course), yet we find it difficult to imagine the subjective quality of that representation in the case of a complex instinctive action performed for the first time. We find it difficult because the goals to which our own purposeful actions are directed are imaged in forms overwhelmingly dependent upon memory of past experiences, and there can be no images with this origin in the case of the first performance of an instinctive action. Among the features which differentiate the human mind from that of the lower animals is the extremely generalized nature

of our instinctive impulses, such as the impulse to seek food when hungry, to escape from danger, to fight a rival, or to mate. The means of achieving these ends is not innate in us in the detailed manner so strikingly exhibited in the instinctive behaviour of the lower animals, notably such animals as insects and birds. Another feature is our enormous capacity for associative memory, which ensures that when we have reached the age when introspection becomes possible we have already accumulated such an immense stock of remembered experiences, whether directly, or vicariously by communication from our fellows, that a multitude of relevant memory images is aroused by any situation which is of importance to us; that is to say, by situations which arouse an instinctive impulse.

Nevertheless, the fact that the human species consists of two classes of members, males and females, provides us with an instance of different instinctive dispositions of which we have inside knowledge. Within the species, there is a difference between the two classes of its members comparable to that between the two genera of wasps, *Pompilus* and *Ammophila*, the one of which responds specifically to spiders and is indifferent to caterpillars, and the other attacks caterpillars but pays no attention to spiders. In the human species, members of each class are perceived by members of the other class with a positive sexual meaning, but to members of the same class they are sexually indifferent. (Homosexual behaviour, so common in other mammals also, does not invalidate this argument; the essential fact is this difference of meanings, not whether it is universal or absolute.) It is true that the conative side of human sexual behaviour is not innate in so detailed a way as that of other animals, or as the behaviour of the wasps towards their prey. The emotional quality and the most general features of the sexual behaviour of each sex to the other are, however, undoubtedly innate, though both are highly modifiable by experience, whether direct or through the mediation of communication by others.

We must therefore conclude that the course of embryonic and post-embryonic development (which includes the operation of the endocrine glands) can produce a Central Agent such that its sensa can be experienced as meaning action directed towards anticipated ends which have never yet been experienced. No doubt, by experience the ends gain enormously in detail and precision. Whatever the subjective quality of the anticipation, it must, how-

ever, be such, both in instinctive and learnt behaviour, that the animal appreciates whether its action is leading to its realization or not.

4. *Hormic goals and biological consequences*

In order to distinguish between the vague, and surely unjustifiable, use of the word 'purpose' in such a phrase, 'the purpose of the sexual instinct is the continuance of the species,' and the precise and justifiable statement, 'the purpose of the animal under the sexual urge is to mate,' we may describe mating as the 'hormic goal' of sexual activity; there is an agent striving to that end. The continuance of the species, on the other hand, may be called the biological goal or 'biological consequence' of sexual activity, because although sexual activity serves that end, we can identify no agent striving towards that end. There is no agent to which the biological consequence of mating is a hormic goal; there is no agent that achieves satisfaction by bringing about the continuance of the species—at least, no agent that science knows anything about. Our conception of a Central Agent does not involve the notion that among its activities is the direction of all physiological processes to the conservation of the life of the organism as a whole. We may take it that the regulation of breathing by the nerves and muscles concerned, or of the composition of the blood by the kidneys, is carried out by agents whose hormic goals are confined to their own acts and do not include the continuance of the life of the organism.

When interpreting the instinctive activities of animals it is essential to bear in mind the distinction between hormic goals and biological consequences, and the fact that the activities which are satisfying to the animal are directed to the former and not to the latter. The fact that a *Sphex* wasp may sometimes go to the labour of sealing up its nest though its contents have been removed by the human experimenter has been cited as an example of the stupidity of instinct. But we may take it that the wasp is not engaged in providing for the next generation. It is engaged in nest construction, in finding and stinging its prey and placing them within the nest, and finds these activities satisfying in themselves. And in this respect human beings are no different: they enjoy their instinctive activities for their own sake. Men do not regard love-making as a labour which it would be stupid to undertake under circumstances which cannot lead to the production

of offspring. A wasp elaborately sealing up an empty nest may be guilty of self-indulgence, but it is scarcely fair that it should be accused of stupidity by a member of a species which has made a fine art of the enjoyment of its instinctive activities divorced from their proper biological consequences.

At the moment we are concerned only indirectly with biological consequences. We are not concerned with how it comes about that the acts of an agent, or of a number of agents collectively, are directed to hormic goals having remote results of importance to them, or even to organisms other than the agents themselves (such as their offspring). This belongs to the theory of evolution, and will be discussed later. It may be noted here, however, that we seem to be left with the alternatives of (1) natural selection of random variations of hormic goals which has brought about the survival of only those organisms whose hormic goals happened to have these remote consequences; (2) an agent, unknown to science, to which these biological consequences are hormic goals, and which uses the organisms as means to achieve its ends; (3) some other, unknown, factor in evolution. I have omitted Lamarckian inheritance as an alternative, believing that even if it is a fact it does not provide an adequate explanation (chapter vi).

Hormic goals themselves require a further classification into immediate and terminal. When a bird sets out to build a nest of the form characteristic for its species, it is probably necessary to assume that it has some foresight or anticipation of the form the nest is to take. It may be that the action involves from the start not only this anticipation, but also anticipation of the process of incubation and rearing the young. It may involve this, but it is unnecessary to assume it. It may be that the hormic goal to which the first acts are directed are simply the completed nest (the immediate hormic goal) and that the attainment of this evokes further hormic goals, the terminal one of which is the launching of the young birds into the world. In very primitive animals, the hormic goal is possibly always only a little ahead of the present action. This is not to be conceived in the form of the chain-reflex theory of instinctive action, but rather on the analogy of many of our own consciously purposeful actions. In many of these we have no clear idea at the outset what the final result of the whole business is to be. We have to allow the action to develop from stage to stage. If we start to solve a complex logical

or mathematical problem, we proceed step by step and arrive at a final solution which may be correct, but was quite unforeseen at the beginning and may indeed be very surprising to us.

There is, however, abundant evidence that animals at least as low in the scale as insects may direct their actions to comparatively remote, well defined, goals. This can be demonstrated by interrupting the normal course of the instinctive action and observing how the animal deals with the situation. Instances of the purposive adaptation of insect behaviour to special circumstances, requiring sometimes action directed to ends only attainable after a long series of actions, abounds in accounts of the behaviour of solitary wasps and bees.¹¹ This can be illustrated by some observations of McDougall (1931). They refer to a mason wasp, which constructs a clay nest consisting of a cluster of cells. These are constructed successively. In each an egg is laid, and about 30-40 small paralysed spiders are deposited in it; the cell is then closed with a lid, and another cell is started. Each cell is built from below upwards, and is stocked through the open upper end. A cell is built of pellets of clay which the wasp lays smoothly along the free edge of the growing cell. The following is an abbreviated account, mainly in the observer's own words, of an experiment carried out on one wasp.

When it had almost completed the fifth cell of the cluster, a small hole was made by the experimenter through the wall of the cell. Returning with a pellet of clay to continue the construction, the wasp seemed disturbed; instead of applying the pellet to the growing margin of the cell, she fussed round the cell for a while, then entered it, placed her pellet on the margin of the hole, came out and flew away. Presently she returned with another pellet, again entered, and placed it beside the last one; repeating this with a third pellet she completely closed the hole, and at once returned to work on the margin of the cell.

When one cell was half stocked with spiders, the experimenter made a hole in the bottom of it and removed all the spiders together with the egg. On returning with another spider, the wasp seemed agitated. She placed the spider in the cell, then fussed about, climbing all over the cell and frequently entering it. Presently she removed the spider, flew away with it, returned and replaced it in the cell. Then she removed it a second time, flew far away, and returned without it. She climbed over the cell

11. For a general discussion of this see McDougall (1923).

and thrust her head into the hole at the bottom. She then flew away, returned with a pellet, and with it neatly plugged the hole from the outside. After this, instead of resuming at once the task of stocking the cell, she brought about sixty pellets which were plastered in various positions on the cluster of cells as though to strengthen it generally. Next day she re-stocked the cell with spiders. The same wasp was subjected to various other trials.

Commenting on these observations, McDougall says: 'They show first that the whole activity of cell-building has conative continuity; secondly, that this conation is satisfied only by the completion of an intact cell; thirdly, that, when the wall of the cell is partially destroyed, the wasp appreciates the fact, and, interrupting the normal course of building, repairs the breach; fourthly, that she has insight into general relations of the cell, the egg and the spiders with which she stocks the cell, an insight limited it is true, yet generally sufficient to enable her to rectify any gross disturbance of the normal course of the whole process under the guidance of foresight of the completed whole.'

Another example of wasp behaviour implying an anticipation of the course of action necessary to achieve its goal may be taken from the Peckhams' well-known book on wasps (p. 303). A wasp of the species *Pompilus sceleratus* brought a large spider to her nest, and tried to pull it in, but was unable to do so as the entrance to the nest was not large enough to admit it. 'She pushed it out and carried it to a place of safety up among some clover blossoms. She then washed and brushed herself neatly, and took several little walks, so that it was fully fifteen minutes before she began to enlarge her nest. All that time she must have carried in her little scrap of mind the idea of doing a necessary act which was outside her ordinary routine.' Having enlarged the opening to her nest, she successfully got the spider into it.

These instances of instinctive behaviour implying anticipatory images, or anticipations in some form, taken from wasp behaviour are, it is true, examples of the operation of psychical factors more highly developed than usually detectable in insect behaviour. They demonstrate, however, that it is not permissible to deny purposive action directed even to distant goals, the achievement of which requires a long train of complicated acts, on the grounds that the agent had no prior experience of the goal or of the way to achieve it. And if we have to admit it for these complex instances, we must admit it also, in its degree, for the simplest forms of instinctive behaviour.

CHAPTER II

THE UNITY OF THE ORGANISM. BIOLOGICAL FIELDS

1. *The synthesis of an organism out of its parts*

IN THIS chapter we shall deal with some of the features of the organization or 'wholeness' of living organisms. The interpretation of these in terms of the organism as a nexus of subjects must be left to chapter III.

Nearly all writers on the subject agree that the notion of organism is not peculiar to biology. It is exemplified, for instance, in an atom or a molecule, where the total system of forces acts causally as a unit, both on its own parts and on external systems. Nevertheless, the living organism is the organism in its most developed form and it was consideration of it that was responsible for attempts to formulate principles of 'organism' as represented, for example, in the works of J. S. Haldane. For this reason, and because we are primarily interested in living rather than in non-living organisms, we must deal briefly with some of the features of living animals in their character of organisms or wholes. At this stage we shall not consider the parts of the living organism below the level of the 'living' parts (agents) which compose the organism as a whole.

In formulating any theories of the unity of the living organism it must be borne in mind that this unity is not primary in the sense that it cannot be synthesized out of separate living parts.

To some extent this synthesis happens in the life history of every animal. Embryonic development is characterized by the subdivision of the egg into agents which exhibit for a time a very considerable degree of independence of the other parts, or of the whole. This is illustrated by the well-known transplantation experiments. For instance, an amphibian limb-rudiment, transplanted to a foreign site such as the head, continues to develop as a limb. In fact, such parts will often develop when removed from any connection with the rest of the body, provided they are supplied with a suitable nutritive medium. The relation of these self-differentiating embryonic parts to the rest of the embryo is little more than that of parasite to host. They draw their nourish-

ment from it, but are not dependent on it for factors determining their own further development.

Comparatively late in embryonic development, these essentially independent parts or agents become connected up into a new unity by the development of the nervous system; in other words, by a complex system of intermediary agents, the neurones. But this new unity does not abolish the previously essentially independent agents. It is a unity achieved partly by the formation of a new connection between these agents allowing of a more specific mutual interaction between them, and partly by the development of a dominant Central Agent which responds to stimuli transmitted to it by other agents, mainly the peripheral neurones. The response of the Central Agent to the stimuli thus provided to it is to supply stimuli to which other agents, the effectors, respond. The nervous system, however, is not the only unifying factor in the adult animal. The hormone system must be reckoned as one of them. The unitary factor present in the developing embryo in the form of morphogenetic fields is also clearly present in the adult, though more easy to demonstrate on some organisms, such as planarians and newts, than in others, such as frogs and mammals.

Experimentally, this synthesis of an organism out of separate parts can be carried very far indeed. In newts, limb-buds of different embryos can be interchanged and will develop into functional limbs in their new sites, become connected with the nerves and operate under the control of their hosts, as if they were their own proper limbs. Sections of the spinal cord rudiment can be taken out of one embryo and substituted for a similar length removed from a second embryo. This foreign piece will join up with the spinal cord of its host, and take its place as part of its functional central nervous system. Heart rudiments can be interchanged between embryos, and will develop and function as if they were the original hearts of the animals in which they are now situated.

These and many similar experiments demonstrate that the capacity for synthesis of separate parts into whole living organisms is much greater than is revealed by the integration of previously essentially independent parts in normal embryonic development. They also show that it is not necessary that the parts should even be derived from the same egg. All the above mentioned examples of transplantation (limbs, spinal cord, heart) can be successfully carried out between animals of different species—for instance,

between species of the genus *Amblystoma*, one of the Amphibia. No doubt, the capacity for entering into the relations necessary to produce by synthesis a living whole depends upon a similarity of organization (including chemical organization) between the ingrafted part and its host, which is ultimately traceable to descent from a common ancestor, though in the case of different species, an enormous number of cell generations has elapsed since the egg from which they trace their common descent.

Limb-buds, spinal cord and heart rudiments are all products of a comparatively late stage of embryonic development, and consist of organized cell masses whose future differentiation into limbs, spinal cord, and heart, has already been determined. It is, however, possible to use much more elementary parts to synthesize an embryo.

The egg of the sea-urchin, *Paracentrotus*, in the 16-cell stage consists of three tiers of cells, a ring of eight mesomeres above, four macromeres in the middle, and four micromeres below. Individual cells, or clusters of cells, can be separated in this stage and artificially united. Hörstadius made composite embryos by uniting separated parts of the same or different embryos. Provided they contain representatives of all the three types of cells, and subject to certain limitations as to the relative orientation of the pieces in the composite embryo, these will develop into normal larvae. For instance, a compound embryo formed out of the eight mesomeres of one egg together with four of the mesomeres and the four macromeres and four micromeres of another egg develops into a normal larva—and this despite the fact that the proportion of mesomeres to the whole is three-quarters instead of the normal one half.

Finally, we may mention the experiments of J. S. Huxley (1911) following experiments by H. V. Wilson. He chopped up a simple form of living sponge, and pressed the pieces through fine silk gauze. By this means the sponge is broken up into fragments varying from single cells to clumps of fifteen to twenty cells. These settle as a sediment on the bottom of the watch glass containing sea water in which the experiment is carried out.

Presently the cells begin to creep together, and out of the sediment little clumps and balls are formed, each of which may re-develop into a functional sponge. All the different kinds of cells, which in the normal sponge are arranged in definite tissues, are at first mixed up anyhow in these clumps. They soon begin to sort

themselves out and take up their proper positions. Certain cells migrate to the exterior and join up to constitute the dermal epithelium, forming a continuous outer envelope to the inner mass of cells. Then certain other cells secrete the calcareous spicules which form the supporting framework of this species of sponge. A central or gastral cavity appears in the inner mass of cells, which form themselves into a regular lining to the cavity, and reveal themselves as the feeding cells, or choanocytes, of the sponge—later still, the opening or osculum appears at the end of the now cylindrical sponge, pores open in its walls, circulation of water starts, and we now have a functioning sponge reconstituted.

There can be little doubt that nothing but technical difficulties stand in the way of our synthesizing a human being by putting together separate cells from a thousand different human beings, or, at any rate, a thousand human embryos.

The unity of the adult organism, composed of billions of cells constituting the various organs and tissues, is therefore not solely or necessarily a unity persisting from the egg throughout embryonic development. It is a unity which is partially achieved during normal embryonic development by the formation of new relations between self-differentiating parts, and which can be achieved in a more radical way by the experimental bringing together of separate cells or larger parts. Thus the unity of a complex organism, whether it be the lower grade of unity dependent on biological fields, or the higher grade of unity of a subject, is not primordial to the organism as a whole. Its source lies in a property of its parts, which at present may merely be stated as the potentiality of entering into relations with other parts to form a whole. The aphorism opposed to the old Cell Theory, that its cells do not make the organism but the organism makes its cells, is only partly true. It is true that the parts out of which the adult organism is synthesized, or can be synthesized, were originally formed by subdivision of a complete organism, the fertilized egg, though this may be many generations removed. Upon this fact depends the similarity of organization which allows them to unite to form a unitary organism. But there need be no continuity of organization of the whole between the egg and the adult.

Thus in this sense the unity of a living animal is not different from the unity of a molecule. As the latter can be synthesized from separate atoms, so in principle, and often in practice, an animal can be synthesized from separate cells. It is true that at present

we cannot synthesize a living animal except out of parts that are already living, and taken from other animals of the same or not too dissimilar species. At present it is not possible to synthesize cells or any other type of elementary living organism out of non-living parts. But whether it will ever be possible to do so or not, it seems reasonable to conclude that lack of technical knowledge is the only obstacle. It seems impossible to escape the conclusion that such a synthesis of elementary living organisms out of non-living parts has taken place in nature. Moreover, as will be discussed in chapter III, it is possible that the difference between living and non-living is to be regarded as one of degree and not of kind, in which case the distinction between them, though a practically useful distinction, is not one which suggests any theoretical obstacle to the artificial synthesis of living organisms from non-living parts.

2. *Biological fields*

No discussion of the factors on which depend the unity of the organism can proceed far without encountering the very important conception of biological fields. The term 'field' is of course taken over from physics; it is essentially an organized distribution of energy, the intensity and direction of which can be measured by the movements of bodies in various parts of the field.

A region carrying a biological field is supposed to be a region characterized by some community or organization of processes distinguishing it from other regions. The term 'field' is suggested by the fact that in many cases the activity of the region shows a graded intensity from some point. This may be made visible directly by graded deposit of substances such as pigment, or indirectly by the responses of cells or other agents within the field.

The concept of biological fields owes its origin largely to the work of Child (summarized by him in 1924) and has received much attention from biologists during the last twenty-five years. The simplest type of such fields is the axial gradient field, in which there is a decrement of intensity of field action from one end of the region carrying the field.

Axial gradient fields can be exemplified by certain phenomena of regeneration in worms.

Many kinds of worms if cut in two will regenerate a tail on the hind end of the front piece and a head on the front end of the hind piece, thus producing two functional worms. This applies

only if the cut is within a certain distance from the middle of the body. If cut in two very near the front end, a head may regenerate at the hind end of the front piece, forming a short worm with a head at each end. Similarly a short piece cut off from the hind end regenerates a tail at the cut surface, forming a double-tailed piece. Thus there is a gradient of potentiality for head formation falling from the anterior to the posterior end of the worm, and a gradient of tail-forming potency in the opposite direction. These are so balanced that about the middle of the worm either a head or tail will be formed and thus supply the missing part to each piece, but near the front end only a head, and near the hind end only a tail, can be produced. These gradients of head and tail potencies have been analysed in detail in a fresh-water relative of the earthworm, *Lumbriculus* (Haffner).

Examples of complicated actions of biological fields are afforded by the constitution of fragments of planarian worms (flat worms). Owing to their great capacity to reconstitute a whole animal from a piece cut out of them, they have been the subject of many experiments. If a planarian is bisected longitudinally, each half will reorganize itself into a complete animal with symmetrical and properly proportioned organs.

A variation of this experiment was performed by Steinmann. He cut the head off a planarian, and then split the animal lengthwise for a short distance down from the transverse line of the cut edge, giving a Y-shaped organism. The stem of the Y consists of the main part of the body, and each limb of the Y forms, so to speak, a headless neck. A new head is formed on each of these, so now there is a double-headed worm, each head attached to the body by a short 'neck.' The animal does not long remain in this condition, however. It 're-individualizes' itself in one of two ways. If the longitudinal cut was not central, so that one head is distinctly smaller than the other, this head and its neck are gradually absorbed into the body of the remainder. If the two heads are of approximately equal size, the two necks gradually grow together from behind forwards. This is followed by fusion of the two heads. This process is necessarily accompanied by extensive remodelling of the parts. For example, the head of the worm carries two eyes. As the fusion of the necks proceeds, but long before the level of the eyes is reached, the inner eye on each head begins to diminish. By the time the fusion has reached the level of the eyes, and the formerly Y-shaped animal has become

a single worm except for a slight notch at the extreme front of the head, the two inner eyes have become reduced to mere specks, and finally they disappear altogether, leaving a normal head carrying two eyes. A complete single individual has been re-formed.

These cases present an analogy with the return to equilibrium of a physical field after deformation by an external force: return to equilibrium meaning a redistribution of energy so that the potential energy of the system tends to the minimum which circumstances permit.

It is easy to imagine, or to construct, such systems which will behave in a manner suggesting an analogy with the re-individualization of a planarian, having due regard to differences in complexity. Let us adapt, for an illustration, the example given by Petermann in his critical discussion of the Gestalt theory of psychology, which as we shall see is based upon the field concept. If there are five equal floating magnetized needles with the north poles uppermost, and suspended above them a fixed magnet with its south pole downwards, the five floating magnets will take up their positions as the points of a regular pentagon around the fixed magnet as a centre. Variations in the initial arrangements of the magnets will affect the routes by which they attain their positions in the pentagon, but will not affect the shape and size of the final figure. If one of the floating magnets is pushed in towards the centre of the figure so as to make an indentation in the pentagon, and then released, there will be a general movement of the magnets, which will re-form the regular pentagon. The pentagon 're-individualizes' itself. The size of the pentagon can be altered by altering the strength of the central or the floating magnets.

The conception of an atom as a vibrating electrical system implies that all matter carries at least an electro-magnetic field. 'If the electro-dynamic theory is sound, the characteristic relationships of the elements of any biological system is a function of the field of the system. If this be true, then the great jump from living organic matter to non-living physical matter is no longer inexplicable. The difference between the two is to be found in all probability in more complex fields and more complex molecular structure' (Burr and Northrop).

It is easy, however, to give far too simple a form to the idea that the wholeness of a living organism, and especially its capacity for compensating for deformations of its structure or for enforced alterations in its normal metabolic processes, is referable in

principle to the same factors as those which constitute the wholeness of a molecule, or of any dynamic physical or chemical system. On the assumption that the electro-magnetic field of matter is due to the movements of electrons, then the disturbance due to the introduction of another body into the field causes an automatic reorganization of the whole field on principles which are illustrated in essentials by the parallelogram of forces. But the field with which a living organism, or living part of an organism, is 'charged' operates on the vital level in a different manner. The movements and differentiations of cells and cell-aggregates in the regeneration of a head or a tail in the instances we have given are not referable to the resultant of the forces in the field in the way in which the movements of the members of the floating pentagon of magnets are brought about. These movements are the result of all the magnetic fields of the whole multitude of moving electrons in the system. Biological fields, although on the physical level they doubtless have the same nature as physical fields, in their mode of action they are 'stimulus fields' (Reizfeld of Gurwitsch). Each living agent (cell or other living part) is indeed part of the carrier of the field, which acts upon it and upon which it acts. But the physical result of their mutual interaction is not directly the cell movements and differentiations which produce, for instance, a new head. The alteration in the physico-chemical processes of the agent caused by its interaction with the field is to the agent a stimulus to which it responds. Its response is determined by its specific organization and has no direct quantitative relation to the stimulus, which is a signal to the agent for a certain type of action which it carries out by its own organized store of energy. In other words, the relation between stimulus and response is mediated by an act of perception.

The extremely indirect way in which physical disturbances in the normal functioning of the body may be compensated is illustrated by the process of regulation of the pressure of carbon dioxide in the blood. If this is increased by muscular activity, the excess is got rid of by accelerated respiration. The increased carbon dioxide diminishes the alkalinity of the blood. This acts as a stimulus to motor neurones of the respiratory centre in the brain. The neurones respond to this stimulus by discharging nerve impulses which in turn provide the stimuli to muscle fibres of the respiratory muscles, to which they respond by increased activity. Respiration is thus accelerated, and so more air is passed through

the lungs in a given time. The diffusion of the excess of carbon dioxide from the blood into the lungs, and its subsequent removal from the body, is thereby brought about. In this process there is plainly no physical congruity between the decreased alkalinity of the blood and the chain of processes by which the normal alkalinity is restored.

Biologists will recognize the regulation of carbon dioxide in the blood as the main argument on which J. S. Haldane, with much greater elaboration and incomparably greater knowledge, bases his theory of organism as contrasted with theories of mechanism and vitalism. As he says (1928, p. 88), 'there is no definite chain of physico-chemical causation between a certain definite hydrogen ion pressure or deficient oxygen pressure and the activity of the nerve-centre in the brain.'

Nevertheless, biological fields must probably be looked upon as primary factors in the wholeness of living organisms, although their action is not direct but in the form of providing stimuli to which the living sub-agents respond. The fertilized egg, before it starts its development, carries a field which is often made visible by locally graded concentrations of material deposits in the cytoplasm of the egg. Ultimately, all movements and histological differentiations of cells or cell-groups of the developing embryo must be interpreted as responses to this stimulus field, which becomes more and more complex as the embryo develops and the carrier of the field becomes more and more heterogeneous, sundering the original field into sub-fields. We must leave a more adequate account of this process to chapter v, noting meanwhile that this type of field is chiefly of importance in embryonic development, where they are called morphogenetic or embryonic fields. We may note also that as we can synthesize the electromagnetic field carried by a molecule by bringing atoms into appropriate relations, so we can synthesize morphogenetic fields by bringing separate living parts into appropriate relations. This is exemplified by the experiments of Huxley on sponges and of Hörstadius on echinoderm eggs mentioned above.

Morphogenetic fields, though their action is naturally most conspicuous in embryonic development where morphogenesis is proceeding most rapidly, persist in the adult in various degrees of potency in different species of animals. They are obviously active in planarians and in all animals capable of a large amount of regeneration. In animals such as birds and mammals, morpho-

genetic fields seem to be of restricted potency in the adult—or else the capacity of the living agents to respond to them is very low. They are manifested, however, in all cases of wound-healing.

3. *The brain field*

Besides morphogenetic fields, there are other types of biological fields in the adult. One type of such field, important for our purposes, is the brain field¹—the psychophysical field of Gestalt psychology.

The existence of any physical field is directly demonstrated by the fact that movement of bodies in the field are related to their positions in the field. There is, of course, no question of observing actual movements, whether molar or molecular, within the brain field; nor can we directly observe any other kind of responses of bodies in this field. We can, however, deduce such responses on the part of motor neurones within the field from the movements of the muscles they supply. Moreover, Gestalt psychologists have shown that many subjective phenomena, especially of visual perception, find a simple explanation on the hypothesis that their physical correlates in the brain are disturbances in a physical field which tends to return to a state of equilibrium in the sense of a condition of least potential energy possible under existing circumstances.

The picture which we have to form of the structural basis of the brain field, that is to say, of the carrier of the field, is familiar. The structural elements are the neurones, each consisting of a functional centre, the ganglion cell, which is produced into fine processes. One of these is the axon (which, when it is long, is called the nerve fibre). The others are the dendrites. Near its end the axon divides into fine branches which communicate with other neurones, either with the bodies of the cells or through the intermediation of their dendrites.

When a neurone is excited, it initiates nerve impulses which pass down the axon. These, reaching the other neurones with which the terminations of the axon are in contact, act as a stimulus to these neurones. The latter respond to this stimulus by in their turn initiating nerve impulses which pass down their axons and excite other neurones.

The neurones with their axons and dendrites were formerly regarded as structural units whose function in mediating between

1. The use of this term does not imply any discontinuity with the field carried by the entire nervous system, and includes the differentiated portions of the field constituting the cortical or lower brain centres.

sensory stimulus and motor response is solely to conduct nerve impulses much as wires conduct electric currents. The ganglion cells on this analogy can be compared with storage batteries, which release their own current owing to some trigger action set off by the action upon it of a current reaching it from another neurone. The actual path from neurone to neurone along which the impulse travels depends, according to this view, on the relative resistances at the synapses—the points of junction of an axon with the next neurones in the chain. This is the picture which a rigid associationist psychology forms of the nervous mechanism of behaviour. The nerve impulse initiated in a receptor organ travels to its appropriate muscles by paths of low synaptic resistance predetermined in embryonic development in the case of reflex or instinctive action, or formed as a result of previous activity in the case of learnt behaviour.

This picture was helped by the belief that there is protoplasmic discontinuity between the ends of the axon branches and the dendrites (or the body of the ganglion cell) with which they are in contact. More recent work, however (e.g., Tiegs), has shown that this applies only on the anatomical level of neurones. On the level of the neurofibrils contained in the neurones, the whole nervous system must be looked upon as a syncytium, for the neurofibrils run continuously from one neurone to the next through the synapse. There is, however, functional discontinuity at the synapse in regard to the passage of nerve impulses, since these do not pass across the synapse from one neurone to the next; a volley of impulses transmitted along the axon of the first neurone excites the second neurone to initiate nerve impulses itself. Moreover, nerve impulses can be propagated along a nerve fibre in either direction, but are relayed in only one direction across a synapse.

But, as we shall see, the phenomena studied by Gestalt psychology and the results of removal of portions of the cerebral cortex require for their explanation the assumption of a form of nervous activity additional to the initiation and propagation of nerve impulses; they require the assumption of local disturbances spreading over a physically continuous substratum, and it is perhaps permissible to look upon the network of neurofibrils as this substratum. On this view, therefore, this network is the carrier of the brain fields about to be discussed, but naturally the reality of these fields does not depend upon the correctness of this identification of their carrier.

4. *Gestalt psychology and the field concept*

This system of psychology, which uses the notion of physical brain fields as its main explanatory principle, was applied at first to the organization of sensory fields, but was later developed, especially by Köhler and Koffka, towards a complete explanatory account of mental processes and behaviour. The following account of certain aspects of this system of psychology is based mainly on the works of these two authors, references being to Köhler's *Gestalt Psychology* (1930) and Koffka's *Principles of Gestalt Psychology* (1935).

The Gestalt conception was founded upon consideration of visual phenomena. It was found, as will be indicated below, that these phenomena display characteristics similar to those found in certain physical systems, especially those whose changes are governed by the principle that their potential energy tends to the minimum that existing circumstances will allow. This similarity is considered to be more than an analogy. The field properties of phenomena as experienced are believed to be due to the fact that these phenomena are the correlates of physical fields in the brain. Hence the total brain field is called the psychophysical field. Any segregated sub-field in this total field is a Gestalt. Thus a seen figure on its background is an example of a Gestalt. It is a sub-field of the total field maintained by local stimulation, with of course mutual reaction between it and the total field of which it forms a segregated part.

To quote from Köhler (p. 148), 'the word "Gestalt" means any segregated whole . . . wherever a process dynamically distributes and regulates itself, determined by the actual situation in a whole field, this process is said to follow principles of *Gestalttheorie*. In all cases of this type the process will have some characteristic which exists in an extended area only, so that a consideration of local points or local factors as such will not give us full insight into the nature of the process.'

According to Köhler, the relation between the pattern of retinal stimulation and the distribution of the resulting processes in the psychophysical field must be interpreted in the following way (pp. 107-109): Under the influence of the rays of light reflected from an object, the retina is a mosaic of indifferently related stimulated points, functioning independently. How then is the pattern of stimulation represented in the psychophysical field, if it is not preserved by isolated conduction paths? His answer is,

that if under the circumstances one set of processes remains detached from the rest, as when we see an object standing out from its background, there must be dynamical forces at work. Processes corresponding, say, to a definite coloured area will have definite properties of a class of processes, different from the properties of a class of surrounding processes which corresponds to another colour. They will remain segregated in the nerve network if we suppose that their differential properties provide separating forces of contact, so that they mutually exclude each other.

The symmetry of a seen circle is to be accounted for by surface forces of separation which keep the physiological processes which correspond to the seeing of the circle distinct from the surrounding processes corresponding to the seeing of the ground on which the circle is lying, the dynamical influence exerted by the latter on the former being the same in all directions. Thus the circularity of the seen circle is due to fundamentally the same forces in the brain as the spherical shape of a drop of oil in water, and as in that case, depends not only on the homogeneity of the processes within the drop of oil, but also the homogeneity of the processes in the surrounding field, the 'ground.' He cites in evidence that if the field surrounding the seen circle is not homogeneous the symmetry of the circle may be distorted as in the optical illusion where two parallel lines make a circle appear oblate. Perhaps a more striking and better known example of what is evidently a similar phenomenon is the figure obtained by placing across three parallel lines a series of lines bent like arrow heads, with the points of the arrows lying on the middle of the three lines. Such parallel lines irresistibly seem to diverge in the direction in which the arrow heads are pointing.

Koffka cites a soap bubble as an example of a simple physical system exhibiting the features which govern the distribution of forces in a Gestalt of the psychophysical field. The reason why the bubble tends to a spherical shape is familiar. The molecules of soap forming the film attract each other, and therefore will tend to take up as little space as possible. They will therefore form the thickest film, that is to say, a film with the smallest area, that the pressure of air inside the bubble permits. A sphere is the shape which fulfils these conditions. Such stable physical systems always exhibit the properties that potential energy tends to a minimum, and that spatially they tend to take up simple, regular

and symmetrical shapes. But both these properties are relative only. There will be the minimum of potential energy and the maximum of regularity that conditions allow. Among the conditions must be the degree of heterogeneity of the substrate, and the interaction of contiguous fields.

Let us now consider some of the simpler facts on which it is concluded that subjective sensory experiences are the correlates of dynamical processes of this type.

If we look at a surface the area of which is divided equally between irregular black and white patches, we see it simply as a surface broken up into such patches. But if we look at another surface, also divided equally as to total area into black and white, but in which the black areas are in the form of figures exhibiting some degree of symmetry or regularity, such as circles, crosses and so on, we now see it as a collection of such black figures on a white ground; the white now merely forms the spaces between the figures. If we reverse the areas, so that the white ones have a greater degree of regularity than the black, we see the whole as a collection of white figures on a black ground.

Thus areas exhibiting properties of symmetry or regularity, or of 'good continuation' (e.g., rhythmically undulating curves), are more easily seen as wholes than irregular areas. Another feature which favours this is that the area should be 'closed,' that is to say, that the boundary between the figure and ground should be complete.

Another factor of a different nature, however, obviously favours the unifying of points of stimulation into wholes. This is the factor of familiarity. This is shown by the well-known puzzle pictures, when, for instance, the face of a man is concealed in a drawing of a landscape by making parts of the outline of the face and features parts also of more conspicuous or more integral items in the landscape, such as trees and hills. We may look at this picture for a long time without seeing anything but the landscape. Then suddenly the various lines and shapes forming the man's face seem to come together, and we now see the face standing out so conspicuously from the background that we wonder how we could ever have missed it, and we cannot now look at the picture without seeing the face.

It is of cardinal importance to Gestalt psychology, however, to recognize that familiarity, important though it may be in many cases, is not the primary property which causes a number of points

of stimulation to give rise to a seen whole. An example of the evidence for this conclusion is the fact that if patterns are constructed which contain such familiar shapes as letters, in which the lines of the letters are continued into other parts of the pattern forming regular or closed figures of much less familiar shapes, a person asked to describe what he sees in the composition of the pattern will pick out these closed figures and not see the letters at all. Indeed, even when the fact that certain lines of the pattern form letters is pointed out, it may still be very difficult to see them as such.

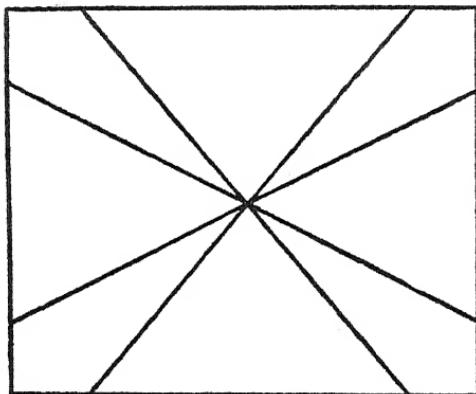
But the fact remains that seen wholes or units, such as an animal or a pencil, do commonly correspond with natural objects or things, and also that we normally see the things and not the ground or spaces between the things. The empiricist explanation of this correspondence is that we have learnt by experience that such things behave as units, and therefore we have learnt to see them as such. Moreover, it is the things that are of practical importance to us, and not the spaces between them. Gestalt psychology rejects this as a fundamental explanation, without denying that learning or experience is very often an important factor. The grounds for this rejection are various. For example, sensory units often exist without there being a corresponding physical unit. A number of separate dots may be seen as a circle, though physically there is only a collection of disconnected points. A physical object does not necessarily correspond to a sensory unit, as where familiar objects are concealed by being made part of a larger pattern. Nevertheless, most natural objects do correspond to sensory units. This is because some discontinuity of optical properties almost universally obtains at the boundary between a natural object and its surroundings. Therefore there is also a discontinuity of the properties of the corresponding brain fields at their areas of dynamical contact. When the discontinuity is not marked the physical object is not seen as a unit. An example of this situation is presented by camouflage or protective coloration in animals. A moth with wings coloured in irregular light and dark patches is not seen when on a similarly variegated background, unless some other factor, such as a movement on the part of the moth, or special attention on the part of the observer, comes into play to emphasize the blurred discontinuity of processes in the psychophysical field corresponding to the ill-defined difference between the optical properties of the object and ground in the 'geographical environment.'

These facts are interpreted as showing that the physiological processes aroused by stimulation of points are not independent but interact to produce fields of force, comparable to—and indeed fundamentally of the same nature as—electromagnetic or other physical fields such as the system of forces in the soap bubble. They therefore tend to fall into regular forms if not prevented from doing so by external stresses. The field processes corresponding to the retinal pattern of our black and white surface is more strongly organized, more stable, in those parts which correspond to the regular areas than in those corresponding to the irregular areas. Hence we tend to see the regular areas as figures, and the irregular areas as mere ground on which the figures appear.

Internal forces in the fields tend to produce simple shapes unless compelled to complexity or irregularity by the stimulus. Koffka produces much evidence for this. For instance, after-images of slightly irregular geometrical figures tend to be more regular than the image produced by the actual retinal stimulation. An after-image of a square will gradually lose its sharp contours and become more circular. In the absence of continued retinal stimulation to maintain the less stable organization, the field tends to a greater regularity and simplicity.

If irregular figures are exposed to an observer for a very short time, and he is afterwards told to draw them from memory, he tends to draw them more regular than they really are.

When a figure is capable of 'good organization' in more than one way, the different possible organizations may fluctuate as we look at it.



If we look steadily at this figure (taken from Köhler) we can

see it either as a cross of four slender arms with pointed ends, or as a cross with four larger sectors familiar as the insignia of certain Orders. As we look steadily at the figure we see one or other of these organizations taking form and attaining a wonderful distinctness, to give way in a moment to an equal distinctness of the other form.

Koffka gives an impressive proof of the tendency of a whole which is strongly unified as regards shape to resist forces which would make it heterogeneous in other ways—in this case, in colour. A grey ring is placed symmetrically on a background half red, half green. The boundary between the red and green parts of the background thus forms a diameter of the ring. As is well known, a grey patch on a red ground appears greenish, and vice versa. But the grey ring under these circumstances will appear more or less homogeneously grey all over. Now lay a narrow strip of paper across the ring on the boundary between the red and green background, thus dividing the ring into two separate semi-circles. At once the grey semi-circle lying on the red ground appears greenish, and the one on the green ground appears reddish. The conclusion is that in the undivided figure the tendency to see the ring as a whole, though due to its simple regular shape, extends also to its colour. But break the ring into two semi-circles, and each will now appear of the colour complementary to its background.

Thus it is a fundamental postulate of Gestalt theory that there is a certain correspondence between phenomena as experienced and the physiological or physical processes underlying them. This correspondence is called 'isomorphism.' Applied to seen spatial order this principle 'will lead to the general statement that *all experienced order in space is a true representation of a corresponding order in the underlying dynamical context of the physiological processes.*' (Köhler, p. 48.) It would take us too far beyond our province to discuss the detailed application of the principle of isomorphism even to visual experience alone. It must suffice to say that 'the mere geometrical localization of the processes in the brain cannot be the correlate of seen spatial order' (p. 174). It is rather a question of the dynamical relations of the brain processes. Moreover, it must be remembered that far more order is experienced than order in space. Certain experiences 'belong together.' The simplest cases are indeed spatial, as those already

mentioned, where groups of separate lines, points and shapes are perceived as forming a geometrical figure or a familiar object. Here the principle of isomorphism assumes that underlying such seen wholes is a spatially continuous physiological process forming an organized sub-field in the total visual field.

But the visual field is not the only sensory field to which such considerations apply. A melody is heard as such, not as a mere sequence of notes. The underlying physical processes form a Gestalt, as in the case of a seen whole, though here there is organization in time instead of in space. Moreover, if while the melody is being played there is an accompaniment of miscellaneous extraneous noises from street traffic and so on, the melody is heard as a whole segregated from its background of unrelated noises, just as we see a figure segregated from its ground.

The principle of isomorphism is, however, applied much more widely than to a congruence between direct sensory experiences and their underlying physiological brain processes. Thus Koffka concludes that the felt intrinsic necessity of a logical conclusion developed from premises corresponds to the intrinsic necessity of the developing physiological field processes. Error in thinking may occur where there is more than one possible organization of the field, comparable to the conditions in the optical field illustrated by the figure on p. 48. Feelings of attention, striving, and purpose are isomorphic with strains and stresses within the psychophysical field which are tending to change the field in the direction of greater equilibrium.

There are, however, clearly very serious objections to using the principle of isomorphism to give a causal explanation of behaviour and logical thinking in physical terms. Quite apart from the fact that if there is a real isomorphism between physical and mental processes, it should be a matter of indifference whether we give our causal accounts in physical or mental terms, there is surely a logical fallacy involved in the argument. For the idea of physical fields and the necessities of their dynamical processes is itself the result of logical thinking, and therefore cannot be invoked to explain how that logical thinking arrived at a correct solution.

There is indeed very much in the application by Köhler and Koffka of Gestalt psychology to behaviour which is quite incompatible with the relation between physical and mental processes as I conceive it. Suffice it to say that these authors are at pains to emphasize that all explanations of behaviour must aim at using

no concepts other than those established in physics. Thus in the system of Gestalt psychology, adaptive behaviour is dependent entirely on the intrinsic nature of the physical processes taking place in the psychophysical field, by virtue of which present processes enter into relation with traces² left by past processes (for both Köhler and Koffka discuss this almost entirely in the domain of learnt, not of instinctive, behaviour, and of recognition on the basis of past experience).

According to Koffka, who deals with this matter very fully, an active process such as a visual Gestalt is under a system of tension between itself and the surrounding psychophysical field, and it 'selects' that trace, the activation of which will give the Gestalt the greatest stability. He emphasizes that the phrase 'the communication between the process and trace was determined by the stability of the former' (p. 599) is not to be interpreted teleologically. 'A process must find its explanation in the dynamics of the system in which it occurs; the concept of biological advantage,³ on the other hand, does not belong to dynamics at all' (p. 600). Again (p. 367), 'All action is a process by which stresses existing in the total field are decreased or removed,' and, more generally, 'I admit that in our *ultimate* explanations we can have but one universe of discourse, and that it must be the one about which physics has taught us so much' (p. 48). If this is so, any feeling of purpose we may have must be simply the psychical correlate of stresses and strains within the physical field which are tending to change in the direction of greater equilibrium; that is to say of the least potential energy which the system permits. I will not enter here into any criticism of these views, since that is implied in the conception of the relation between physical and mental processes, and the efficacy of final causation, developed in the following chapter. These quotations have been given to show that in adopting its description of the brain processes which are the concomitants of sensory perception, I am not adopting the system of Gestalt psychology as a whole.

2. According to Köhler and Koffka, a Gestalt, after it has died down with the cessation of the stimulus, leaves behind it a 'trace,' which is conceived (by Koffka at any rate) as an organized chemical product which facilitates the excitation of a field process similar to the one which produced it.

3. Note that Koffka is here referring to what I have called a biological consequence, not a hormic goal. The teleology we are concerned with in this book is not biological advantage, but the direction of acts to ends, whether these turn out to be biologically advantageous or not.

5. *Brain fields and cortical localization*

The conception that the processes in the brain which mediate between stimulation of peripheral sense organs and behavioural response are of the nature of field processes, rather than of nervous conduction along anatomical connections, is very strongly supported, if not indeed demonstrated, by the effects of removal of parts of the cerebral cortex by operation. We will now leave Köhler's and Koffka's works for a moment to consider some experimental work relevant to this matter.

It has long been known that direct electrical stimulation of particular regions of the cortex produces movements of the trunk and limbs. The part of the cortex which will excite movements in this way is the motor area. Moreover, within this area, regions can be differentiated by their connection with the movements of different limbs and muscles. But although stimulation of these areas excites specific movements, and although these movements are normally associated with these areas, yet they are not dependent in any fundamental way on the localization of these areas. For instance, Graham Brown and Sherrington destroyed the arm area of the left motor cortex in a chimpanzee, with resulting paralysis of voluntary movements of the right arm. In a few months' time, however, recovery was so complete that there was no obvious difference between the movements of the two arms. The arm area of the right motor cortex was then very nearly destroyed by a second operation. This gave the expected paralysis of the left arm, but there was no noticeable change in the movements of the right arm. This shows that the recovery from paralysis after the first operation had not been due to control of the movements of the right arm having been taken over by the cortical area normally controlling the left arm. A third operation showed that the recovery had not been due to regeneration of its proper cortical area destroyed by the first operation. Moreover, the paralysis of the left arm resulting from the second operation also disappeared after a couple of months, and now the ape could use both arms for normal complicated voluntary movements, although the motor areas on which the movements of the right and left arms normally depend had both been destroyed.

This experiment shows that though a particular area of the motor cortex is normally functionally related to a particular limb or group of muscles, yet if this area is destroyed, its function is taken over by other parts of the brain.

The absence of any rigid localization of cortical processes in the rat's brain is shown in much greater detail by Lashley's experiments.

The rats were set to learn to perform simple tasks, such as running a maze or choosing the more brightly illuminated of two passages. In all cases, the incentive was to obtain food, placed at the end of the maze, or in a compartment which could only be reached through the brighter passage. In this last case, an additional incentive to learning was provided by electric grids in the floors of the passages; the grid was charged in whichever passage was the less brightly illuminated one in that trial. Thus the reward of food gained by choosing the correct passage was reinforced by punishment in the form of an electric shock following entry into the wrong passage. Lashley refers to this experiment as the brightness discrimination habit.

The rats were held to have learnt the maze after they had made ten consecutive errorless runs, an error being an entry into a cul-de-sac. The rate of learning was measured by the total time spent in the maze, total number of trials, or total number of errors made, before the criterion of learning was achieved. He considers the last measure the most reliable, and therefore only this measure is considered here; the other two measures gave similar results. In the brightness discrimination test the criterion of completed learning was thirty consecutive errorless trials.

The method of training was that commonly used in experiments on animal learning. The rat entered the maze at the end opposite to the food compartment, or entered the brightness discrimination apparatus through an entrance equidistant from the two passages presented for its choice, and was left to find out for itself the correct turns to make in the maze in order to reach the food without wasting time in blind alleys, or the correctly illuminated passage which led to food and not to an electric shock.

One set of rats was trained in these tasks before operation on the brain. The mean number of errors made by this group of rats in the mazes, or the mean number of trials required to learn the brightness discrimination habit, serve as controls for comparison with the performance of operated rats.

Another set of rats had various parts of the brain cortex destroyed, and were then set to learn the same tasks.

Again, intact rats which had learnt these habits, subsequently had parts of the cortex destroyed and were tested to discover

whether they still retained the habits, and, if not, whether they could re-learn them.

In the case of the brightness discrimination test, rats in which the occipital areas of the cortex on both hemispheres were destroyed after forming the habit were found to have lost the habit completely, though injury to any other part of the cortex did not abolish the habit. This is in agreement with the fact that this part of the cortex is the visual area, into which nerve paths from the retina can be traced. But Lashley found that rats from which the occipital cortex had been destroyed *before* they were set to learn the brightness discrimination test learnt to choose the correct passage as quickly as did intact rats—indeed, they actually learnt it with rather fewer errors than did the intact rats. The result of this experiment is therefore similar to that on the chimpanzee. In the normal rat, a specific part of the cortex is involved in learning to discriminate between the degrees of illumination. Therefore if this part of the cortex is removed from a rat which has learnt the brightness discrimination test, it loses the results of its learning. But if the proper part of the cortex is not available for the learning process, any other part can replace it for this purpose. There must, however, be a certain minimum area of the cortex left intact, though the location of that area is not significant. As long as 40% of the entire cortex is left, no matter where it is situated, the rate of learning in this test is unimpaired.

Although in learning the brightness discrimination test a particular part of the cortex is preferentially, though not necessarily, employed, in learning the mazes there appears to be no localization at all of the cortical areas involved. Destruction of any part of the cortex, however, retards the rate of learning as compared with that of normal animals, and moreover the degree of retardation is roughly proportional to the amount of cortex destroyed. In the thirty-seven operated rats used for this experiment, the amount of cortex destroyed (which was always roughly symmetrical in the two hemispheres) varied from 1.5% to 81.2%, with a mean of 31.1%. The average number of errors made by these rats (which had had no experience of the maze before operation) was 78, as compared with an average of 16 for twenty-one intact rats in the same maze. All of them learnt the maze, however (except three which died), even the rat with 81.2% of its cortex destroyed. This rat made 40 errors during the learning process.

As in the experiment on brightness discrimination, Lashley tried the further experiment of training rats to run the maze correctly, then destroying part of the cortex and subsequently testing for memory ('retention') of the habit. In the case of the easiest of the forms of maze employed (maze I) the habit was not abolished by any destruction of less than one-third of the entire cortex. In the case of the most difficult maze (maze III), it was usually abolished by destruction of more than 15% of the cortex, irrespective of the part of the cortex destroyed.

Finally, Lashley performed another test on the effects of cortical destruction on the retention of the habit. Rats with portion of the cortex destroyed, varying in amount and position, learnt to run maze III, and forty days later were re-tested in the same maze. Intact rats tested in the same way served as controls. It was found that the operated rats had forgotten more in the forty days than had the intact rats, for, in re-learning, the latter made only 11% of the number of errors required for their first learning, while the operated rats re-learnt after 33% of the number of errors made in their first learning.

From all these experiments, Lashley concludes that the higher level integrations in the brain are not dependent upon localized structural differentiations, but are functions of some more general dynamic organization of the entire cerebral system. He concludes that motor paths become sensitized to a 'pattern of excitation' so that they will respond to this pattern in whatsoever part of the nervous tissue it may occur. The ease or rapidity with which this sensitization takes place, that is to say, the rate of learning, is nevertheless affected by the total amount of cortical tissue available.⁴ In the tasks which he studied, however, the capacity to learn was not abolished by destruction of even as much as 66-81% of the cortex.

Pavlov removed parts of the cortex of several dogs which had learnt the meaning of various stimuli used as signals that food was about to be presented (had formed 'conditioned reflexes' in Pavlov's terminology). His results are not so clear cut, nor so extensive, as Lashley's. In general, however, removal of any part of the cortex was usually followed by complete loss of all previously

4. It is perhaps significant in this connection that the power of learning by experience in different species of animals is correlated with the size of the brain; this is evident in mammals. On the other hand, complexity of instinctive behaviour shows little or no relation to the size of the brain, as illustrated by such animals as ants, many species of which are exceedingly small.

formed conditioned reflexes, but after periods varying from a few days to several months they could be re-established, though often not with the earlier fine discrimination between stimuli.

6. *Some general features of the psychophysical field*

Certain other conclusions can be drawn regarding the nature and operation of brain fields as inferred from the observations of Gestalt psychologists and the experiments of Lashley.

The main characteristic activity of the nervous system studied by physiologists is the initiation and conduction of nerve impulses. But this cannot be the only type of physiological processes taking place in neurones. There must be at least their own intrinsic metabolic processes. It would seem that there must be added or included the processes which are responsible for the brain fields. As Lashley points out, the physiological processes in nervous activity which have these dynamic field properties cannot be interpreted solely in terms of impulses propagated along nerve fibres. There is yet, according to Lashley, no clue to the nature of these dynamic forces, but they must distribute themselves over the nervous network independently of anatomical conduction paths. The cortical lesions he made in his various operations collectively cut through all the long association tracts in the cortex without abolishing the capacity to learn the maze.

We shall meet with another example of a specific activity of the nervous system other than the conduction of nerve impulses, in Weiss' conception of the modulation of a motor neurone by its muscle (p. 82).

The demonstration of these features of neural activity, not of the nature of the nerve impulses but influenced by the reception of nerve impulses and often issuing in the emission of nerve impulses, is of the greatest importance for our future discussions.

Another feature of brain fields remains to be discussed here. As we have seen, Gestalt psychology developed out of a study of the organization of the visual sensory field. The field processes in the brain are excited by nerve impulses transmitted from stimulated points on the retina, though, as we have pointed out, the physiological processes which have this property of field organization are not themselves nerve impulses. Sensory perception, however, often or usually gives rise to bodily movements. Therefore not only are sensory fields excited by nerve impulses from the sensory nerves, but they issue in nerve impulses in motor

nerves. That is to say, they excite the motor neurones. In fact, the psychophysical field is a stimulus field. Just as embryonic cells, or organized groups of cells, respond to the stimulus of the field in morphogenesis, so do motor neurones or organized groups of motor neurones respond to the stimulus of the psychophysical field, though it appears that it is not possible to give a physiological account of how the sensory field processes excite the motor neurones. We only know that these field processes are activated by the arrival of nerve impulses from sensory nerves, and may issue in nerve impulses propagated along motor nerves. That there is no direct passage of nerve impulses from the sensory nerves through the sensory brain fields (Gestalten) to the motor neurones is shown by the fact that the intensity of the response has not necessarily any quantitative relation to the intensity of the sensory excitation. A small object seen in a dim light may excite a much more violent motor response than a large, brightly-illuminated object, or a whisper than a shout.

7. The unity of the organism considered as a nexus of subjects

We can now define more closely the problem that has to be faced and the lines on which a solution will be attempted in later chapters.

The organism is a nexus of living agents, of which at least the cells, and the Central Agent of the organism as a whole, are subjects; probably many of the agents intermediate in the hierarchy of organization between cells and the Central Agent are also subjects. Confining ourselves, however, to the Central Agent and the cells, the first problem is the relation between a multitude of subjects and a subject of higher order which is both constituted out of and includes the subjects of lower order. Moreover, these constituent subjects precede, or can precede, in time the subject of higher order, the Central Agent. This probably happens in every embryonic development, for a phase is passed through where the parts of the embryo appear to have relations to each other and to the whole which are loose, and as experimental separation of the parts shows, are not essential. But whether or not this is conceded for normal embryonic development, the essential thing is that the organism as a whole can be constituted experimentally by a synthesis of separate cells or other parts. The relation between the Central Agent and its sub-agents is therefore such that the sub-agents generate, or can be made to generate, the

Central Agent in a manner analogous to the generation of a molecule by previously separate atoms.

After the Central Agent has been established by the sub-agents, it continues to be affected by happenings in the sub-agents. For instance, in the act of perception, processes in distant agents such as receptor cells in the eye and ear are somehow combined together, and with the processes of the Central Agent itself, into a unitary experience, the meaning or significance which the perceived situation has for the Central Agent.

Thus we have to take seriously the fact that the Central Agent is not only affected by what happens in its sub-agents, but is in the first place actually generated out of these happenings.

Another essential fact of which we have to take account is that the unity of the self of which we have direct experience is also a unity in time. The character of the self at any moment is the outcome of its total previous experiences, and such of these experiences as I can remember (that is to say, that I can discriminate from the total mass of past experiences) are my experiences in spite of their being in the past.

The Central Agent is therefore a unity constituted by happenings or events separated both in space and time.

Whitehead's system is eminently appropriate for application to this problem. The stream of experience of the Central Agent (and also of the sub-agents) is a nexus of events, the durations of which are their specious presents. The first event of the new-born Central Agent arose—probably at some late stage of embryonic development—by a 'concrescence,' or growing together, of constituents originating in and transmitted from the sub-agents. Subsequent events of the Central Agent are constituted by constituents transmitted to it, not only from its sub-agents but also from its own preceding events. The constituents which are thus transmitted I shall call 'feelings,' again following Whitehead. In the next chapter the nature of 'feelings' will receive more attention; at the moment it is enough to define them as the constituents out of which a meaningful experience is generated, and in particular that type of experience with which we are mainly concerned—the act of perception.

At each specious present, the relation of the Central Agent to its own past experiences is therefore essentially the same as its relation to the experiences of its body cells a fraction of a second ago (allowing for the time taken for transmission through inter-

mediate agents, the neurones). The Central Agent 'feels the feelings' of its sub-agents in the same sense as it feels its own past experiences. My relation to my subsidiary component subjects is essentially the same as my relation to the subject which was myself a moment ago. The locus of the concrecence of feelings is the psychophysical field, the nexus of processes of special sub-agents, the neurones of the brain.

We are now in a position to return more specifically to our principal thesis as stated in the opening sentence of the book. This will require a closer consideration of perception and causation, and of the way in which the former operates in an organism which is a nexus of subjects. For this, much use will be made of Whitehead's Philosophy of Organism, which has been an important source of the conception of the living organism developed in this book.

CHAPTER III

THE ORGANISM AS A PSYCHOPHYSICAL SYSTEM

1. *Perception and causation*

ONE OF the difficulties in the way of adopting any thoroughgoing theory of the living organism as a psychophysical system consists in the obscurity of the body-mind relation. To form a rational conception of this relation it may be necessary to modify the commonly accepted meanings of the words physical and mental, and in the following pages the concept of 'physical' will undergo a modification along the lines proposed by Whitehead. We may begin, however, by employing the terms in their ordinary usage, and start from the premise that the course of any mental process in a living organism is causally related to physical processes, either directly or through the mediation of previous mental processes which, in turn, were related to physical processes.

The elements we find by analysis of process are events. Following Whitehead's analysis of physical processes we are led ultimately to events of a periodic character, each with its characteristic space-time extension. Examples of such elementary events are light waves and electronic vibrations, meaning by the latter, not vibratory locomotion but a 'vibratory ebb and flow of an underlying energy or activity,' as manifested by the contribution of the electron to the electro-magnetic field (1926, pp. 53, 191). Mental process is also analysable into events, of which the characteristic elementary event is the act of perception.

An act of perception, a percipient event, is physical in its beginning and in its termination. It starts with the reception of the energy of the stimulus, experienced as a sensum, and ends with the transmission of energy which acts as a stimulus to the motor neurones. Although a percipient event is physical in its beginning and in its termination, it is mental in the relating of these two phases of the event. It is by this relating that the percipient event starts as an effect and ends as a cause, and not merely as cause in general, but as the appropriate cause of an anticipated event. Final causation is therefore to be looked for in the process which is the percipient event itself. Efficient causation is the action of one event upon another, and is therefore derivative from final causation.

The idea that final causation is to be found within the course of the event itself raises the very important question of the time duration of events. These are not instantaneous, but require a definite stretch of time in which to realize themselves. Whitehead calls the duration of an event an 'epoch' or the specious present of that event; this is a necessary part of the specification of the event. A light wave from the red end of the spectrum has a space-time extension about double that of a wave from the violet end. It is, however, meaningless to divide the period of a red light wave into two portions, each with the space-time extension of a violet wave. Although it is legitimate to distinguish between an earlier and later part of the period of the wave, the whole period is indivisibly involved in the nature of the wave. The wave is a periodic process with a characteristic space-time extension.

Similarly, in more complex events, a certain duration is required for the realization of the event. Whitehead says: 'There is no such thing as a molecule at an instant. A molecule requires a minimum duration in which to display its character'; and, as Broad points out (1923, p. 403), 'Suppose that a certain kind of atom consisted of a nucleus and an electron rotating about it at a certain characteristic rate, such an atom would need at least the duration of one complete rotation to display its characteristic properties.' Psychological events also have their characteristic durations, as recognized in the psychological conception of the specious present. As in the case of complex physical events, such as a molecular event, a succession of many more elementary events may enter into the constitution of a psychological event such as a single act of perception. In order that it may be a single act, however, all these parts of the total experience must be experienced as a unity¹; that is to say, must fall within a specious present. If we are looking at an object emitting a succession of sparks at the rate of twelve a second, as we see each spark we do not have to remember having seen another like it a moment ago. We experience a *series* of sparks; the experience has the character of a single experience, that of a flickering light. But the sparks which occurred as long as a second ago are not part of the present experience. If we direct our attention to them, we remember them; we do not experience them as part of a present experience. When we see a moving object, if the motion is quick enough for perceptible change to take place within the specious present, we actually see

1. Cf. Broad (1923), especially the section 'Sensible Duration,' pp. 346-358.

the movement. If it is so slow that no difference of position can be distinguished within a specious present we do not see the movement. We can only notice in a subsequent specious present that it has moved.

Many observations and experiments have been directed to measuring the duration of the psychological specious present. The duration undoubtedly varies with circumstances, and with the type of psychological process. For a single act of perception it appears to be normally about a tenth to a half of a second, though some psychologists place the upper limit very much higher. This, however, gives the maximum duration of a single perceptual act, or, as we shall call it, a percipient event. The minimum duration of such an event is also difficult to determine, but the experiments of Dodge show that not less than a tenth of a second is required for the meaning of a printed word to emerge. Meaning can of course be given to visual sensa caused by stimuli lasting for a very much shorter period than this—in other words, objects can be perceived though exposed to sight for far shorter periods than a tenth of a second, especially in strong illumination. In fact, much less than a thousandth of a second may suffice. A familiar example of this is given by the sight of objects illuminated by a flash of lightning on a dark night. This may be accounted for, however, by the fact that the excitation lasts longer than the stimulus, or gives rise to a primary memory image which the observer can study as he studies a perceptual field which persists for that period of time (Vernon, pp. 11-13). In Dodge's experiments, that after-action was cut out by following the exposure of the test word by the exposure of a complicated object which starts another act of perception. Under these circumstances he found that an exposure of about a tenth of a second was required to render the word legible.

The fact that the chain of causation is not continuous in the sense of being infinitely divisible, but must be analysed into finite units each with its specific time duration has very important consequences for the theory of causation. A future, non-existent event cannot be a cause of a present event having a certain character; therefore when action is consciously directed towards a future situation, it is not that future situation which determines the course of the present event, but the present idea or anticipation of the future situation. But the same argument must be applied to the causal action of past events upon the present event. Consider

three successive events, A, B, C, of a temporal, that is to say, of a causal, nexus. The fact that B, a causal link between A and C, is not instantaneous means that A continues to have a causal effect on B after A itself has ceased to exist as such. If B is a causal link between A and C, both non-existent during the duration of B, then both A and C must be 'represented' in event B. They must both be in some sense present in B. In the most developed types of mental processes, we speak of the representation of A in B as memory of A, and the representation of C in B as the idea, anticipation, or purposing of C. But as we shall argue later, memory, ideas and purposes are only special developments of a universal character of events in their relation with those other events which are their causal ancestors and descendants.

Even in a chain of physical causation, therefore, though the links of the chain interlock there is an interval between the points of interlocking. These intervals are the durations of the links—the events themselves. Thus if we wish to avoid a radical discontinuity between the living and the non-living, we can find room for the operation of final causation within physical events as well as in percipient events of living organisms. Final causation, then, whether it is to be confined to living organisms or is a universal feature of the causal process which is the course of nature, is to be looked for within elementary events themselves; physical causation is to be found at the junction or interlocking of events.

This brings us more directly to the system of Whitehead, which deals with the relation between final and physical causation, and therefore with the relation between mental and physical (the 'body-mind problem'). This system also reconciles the fact that all process, whether physical or mental, is atomic, with the existence of 'enduring objects,' that is to say, of nexus of events exhibiting continuity of character such as molecules and human minds.

2. *Whitehead's Philosophy of Organism*

Whitehead's Philosophy of Organism is set out in his three books, *Science and the Modern World* (1926), *Process and Reality* (1929), and *Adventures of Ideas* (1933). It is essential to realize, however, that in this chapter I am using his system as a basis on which to develop the theory of the living organism here adopted. I feel that this explanation is necessary, as although I owe the ideas developed in this chapter to my study of White-

head's philosophy, I do not feel confident that he would accept all the uses I have made of it. Moreover, I feel great diffidence even about those passages which profess to be direct expositions of Whitehead's ideas. Even experienced philosophers have found his system a difficult one. In addition, Whitehead's own approach was originally from the side of physics, and I cannot claim more than an elementary acquaintance with that branch of science. I am well aware of the danger of unconsciously misrepresenting the arguments of an expert in a special branch of science when one lacks adequate appreciation of the reasoning by which the scientific concepts he uses have been reached. I have therefore avoided utilizing these physical conceptions as far as possible. As, however, under his system such physical events as electronic vibrations constitute a class of actualities which enter into the constitution of more familiar objects, it is necessary to indicate the attitude to be adopted to such a question as: do electrons exist, or is an electron merely a concept invented for the purpose of correlating certain observed phenomena into a rational system; that is to say, a system such that, given one event, the occurrence of other events can be inferred? I think it is possible to find an answer to this, even with only a slight appreciation of the physical problems associated with the concept of the electron. In this digression I am not attempting to expound Whitehead's views; I am, however, indebted to Dingle's paper, 'The philosophical viewpoint of a scientist,' without following it in some important respects.

Our conclusion is that electrons, radiation, and so forth, are both discovered and invented, but the same applies to every known object—water, tables, and our fellow men. The primary data for consciousness are, on the one hand, sensa and other feelings; these are our awareness of an external world acting upon us. On the other hand are anticipations and purposes, which constitute our awareness of ourselves as agents acting back upon the external world.

The contribution of the subject to this causal process in which he is a link is to organize his sensa with elements of his effector system and thus determine his own action back upon his external world. Ordinary things which we touch and see are such organizations, which justify themselves pragmatically. They provide an external world in which successful action is possible. Sometimes we organize our sensa into objects which do not stand this pragmatic test. In that case we do not hesitate to abandon them.

We may conclude that we were victims of hallucination, or that we were mistaken in some other way. In science, we may find that the concepts we have constructed, often by a long chain of inference, have to be modified because further experience shows that they do not stand the pragmatic test. The whole external world, with its things which we can touch and see, as well as its electrons and radiations, is a concept derived directly or indirectly from *sensa*, and we judge it to be the real world because, and only in so far as, it is a world in which anticipations and purposes are realized. The fact that electrons are not directly observable does not seem to be of critical importance in this respect.²

As we have seen, the process of nature can be analysed into events. At one end of the scale we find such elementary events as an electronic vibration, or a light wave. At the human end of the scale we have to recognize that the mind of a man can be analysed into a series of events, each lasting for a psychological specious present. In spite of their constitutional atomicity, many natural processes, however, present a continuity of character over long periods. A series of electronic vibrations are so related as to form 'an electron.' The series of human mental events constitute the mind and personality of the man.

This conception of a mind being a temporal nexus of events is important in interpreting the actions of lower animals, of tissue cells, or of embryonic parts. Mental events do not presuppose a mind in the ordinary sense of that word. They do presuppose experience, or feeling (and therefore a subject), but not necessarily that continuity of an experiencing subject which is implied by the term 'a mind.' A mind is constituted when a temporal series of mental events forms a nexus with a certain continuity of character running through it.

How we may look upon the nature of events themselves, and of the relation between them which accounts for the continuity of nature, can be set out in terms of Whitehead's system.

For Whitehead, as the title of his principal book implies, reality is process. He conceives of process as a process of experience or *feeling*, even in the case of inanimate objects.

2. In another article (1940, p. 92), Dingle states: 'The electron is not an "object" like a stone or a star. It is a concept formed to account for certain phenomena.' But why, on his own views, should he draw this distinction? For he says of the concept of an ordinary physical object: 'this is the product of reason acting on the elements constituting the total field of consciousness' (1939, p. 131)—the elements being sense data and feelings. Surely electrons are the products of reason acting on the sense-data provided by a physical experiment.

The process is not continuous, but composed of a series of occasions of experience which Whitehead calls *actual occasions* or *actual entities*. These are the final real things of the universe. They also constitute the elementary class of event. Prominent among the different species of actual occasions are the electronic and protonic occasions which constitute matter, and those actual occasions which constitute the mind of a higher animal or man. As the use of the word 'feeling' implies, an actual occasion is a subject.³ In Whitehead's philosophy, however, as will shortly appear, the relation between subject and object is conceived in an unusual way, of which the relation of knower to known is a specialized development.

The use of the words experience or feeling for an elementary physical event such as an electronic vibration, as well as for an event in the mind of man, is an example of the thoroughgoing unification of nature which Whitehead's system achieves: 'Any doctrine which refuses to place human experience outside nature must find in the description of human experience factors which also enter into less specialized natural occurrences' (1933, p. 223). By experience or feeling, however, Whitehead does not imply consciousness. According to him, this is a feature of only a small class of high grade actual occasions. 'We must bear in mind that "feeling" is here used throughout as the purely general term for any kind of acting or being acted upon, in such a way that the make-up of the subject is affected' (Emmet, p. 142). How Whitehead relates feelings, in the usual meaning of that term, to processes in the inanimate world (and thereby justifies his use of the word 'feeling' for both) will be indicated later. Nevertheless Whitehead's system essentially involves a form of pansychism, in which however consciousness is taken to be a later development in evolution. Although I think that to do so would be to abandon a system which places matter, life, and mind, and efficient and final causation, in intelligible relations to each other, those who cannot follow Whitehead in his pansychism may look upon that aspect of the following description of an inanimate actual occasion as no more than an analogy, useful for illustrating how the constitution of the complex types of actual occasions in the living organism can be reduced to the simplest terms.

The fact that process is 'incurably atomic' has to be reconciled

3. It is in this sense that an actual occasion is an elementary event. As we shall see, the process which is the actual occasion, when considered as an object, can be analysed into parts.

with the continuity of character which we find in natural processes lasting far longer than the duration of an actual occasion. This brings us again to the idea of *nexus*.

What we call 'an electron' is a temporal nexus of electronic occasions, each of very short duration, which is its specious present. A human mind is also a nexus of actual occasions with their own characteristic specious presents. This particular type of temporal nexus showing a continuity of character of the successive actual occasions forms what Whitehead calls *enduring objects*. An electron and a human mind are both enduring objects.

The nature of the causal relation between the successive actual occasions of a temporal nexus is fundamental to Whitehead's system. The general nature of this causal relation can be illustrated by a train of conscious thought which is a stretch of the nexus of actual occasions constituting the enduring object, my mind. Experience tells me that in such a train of thought I am aware that the character of my present thinking is in a causal relation to my immediately antecedent thought which can be expressed in the form that my present thinking contains my previous thought. That previous thought is still operating in the present. This is not the same as remembering my past thought, though I can do so by directing my attention upon it. It is rather that the previous thought is still part of my present thinking. Moreover, I am aware that my present thinking is not a terminus, but is directed towards continuing the line of thought into the future. My present thinking is an actual occasion growing out of the antecedent occasion and directed to determining the character of the next occasion.

The same applies to any actual occasion. Its specious present is for it a transition between two worlds, its immediate past and its immediate future. The past is immanent in the present and this acts into the future. A more precise formulation of this idea must be left till we consider what takes places within the actual occasion itself.

The fact that the world exhibits objects with enduring characters is thus brought into conformity with the atomic nature of process. 'Physical endurance is the process of continuously inheriting a certain identity of character transmitted through a historical route of events' (1926, p. 159). Thus a molecule is an enduring object in spite of the fact that it is a nexus of electronic and protonic occasions. The mind of a man is likewise an enduring object,

although it is a nexus of occasions of experience each enduring for the psychological specious present. 'Our consciousness of the self-identity pervading our life thread of occasions is nothing other than knowledge of a special strand of unity within the general unity of nature' (1933, p. 241).

So far we have only considered the temporal aspects of nexus. Assuming the physically elementary nature of an electron, it is a *single strand* nexus. In this type of nexus the temporal organization is more prominent than the spatial. In other types of nexus, however, spatial organization has to be considered more seriously. Chemical atoms, for instance, contain many strands (electrons, protons). These strands are united into spatial wholes or nexus. This unity is due to the fact that each electronic and protonic occasion experiences the action upon it of the other electrons and protons not as isolated units but as an organized unity, for fundamentally the same reason as we perceive objects as such, and not as collections of points. A nexus is a causal unit to its own constituent actual occasions, and may also be a causal unit to actual occasions outside the nexus.

The word 'event' may be used for any nexus of actual occasions which acts causally as a unit—which in Whitehead's philosophy means being experienced as a unit by other actual occasions, including the actual occasions of the nexus itself. The mind of a man from birth to death is an event, containing events of shorter duration such as trains of thought from premise to conclusion, and ultimately analysable into events with the duration of the specious present. A chemical atomic event is that nexus of electronic and protonic actual occasions which endures for the smallest lapse of time which will give the system its causal character as a chemical atom. The limiting type of event is a single actual occasion. I have not however always found it easy, even in Whitehead's own writings, to distinguish between events which are actual occasions and events which consist of a nexus of actual occasions acting causally as a unit. For many purposes, therefore, the word event is easier to use than actual occasion, and I will use the latter only where it is necessary to stress that the event has the unity of a subject.

The expression 'outside the nexus' used a moment ago can only be used in a qualified sense. For when events in a nexus react with events outside it, by that very act the outside events become united with the nexus into a larger nexus. And since

every known or knowable event in the universe must be in causal relation, direct or indirect, with every other known event, the whole known universe is a nexus. But it is obviously convenient to distinguish within this universal nexus smaller nexus with a greater degree of internal organization and coherence, such as molecules and men.

It is in his conception of what happens within the duration of an actual occasion itself, that is to say, within its specious present, that Whitehead departs most from scientific views of causation. Each actual occasion occupies a certain duration even if it is only the period of a light wave. Ultimately any temporal nexus of events must be analysed into a series of events, each an effect of preceding occasions and a cause of succeeding occasions, with an interval between the effect and the cause which is the duration of the actual occasion itself. It is in this interval, within the actual occasion itself, that teleological causation is to be looked for. The solution of the problem of organism, of the mutual relations of parts and whole, both spatial and temporal, has also to be sought in the nature of the processes which are the actual occasions themselves.

We have to take it as part of the metaphysical nature of the world that completed actual occasions give rise to other actual occasions. The form that an actual occasion will take depends upon its space-time relation to its world of actual occasions which are completing themselves at the moment. But although an actual occasion is conceived as arising out of the total nexus of actual occasions which constitute its own immediately preceding world, in the case of those actual occasions which constitute enduring objects there is a specially close relation with one particular preceding actual occasion which we may speak of as the relation between successor and predecessor. This insures that the nascent occasion will have the same form as its predecessor. Thus an electronic occasion will be followed by another electronic occasion, not, say, by a protonic occasion. The new occasion 'inherits' the *subjective form* of its predecessor. Whitehead relates this to physics as follows: 'The words electron, proton, photon, wave-motion, velocity, hard and soft radiation, chemical elements, matter, empty space, temperature, degradation of energy, all point to the fact that physical science recognizes qualitative differences between occasions in respect to the way in which each occasion entertains its energy. These differences are entirely constituted

by the flux of energy, that is to say, by the way in which the occasions in question have inherited their energy from the past of nature, and in which they are about to transmit their energy to the future.' (1933, p. 238).

The fact that a particular occasion will be, for instance, an electronic and not any other kind of actual occasion depends upon this predecessor-successor relationship. But its behaviour as an electronic occasion will be influenced by its relation to other actual occasions. A 'mental' event in the mind of a man will be followed by another 'mental' event, continuing the experience of its predecessor, but modified by the action upon it of a multitude of other events, such as the continual stream of processes taking place in the bodily organs and experienced as sensa.

When I attempt to describe the course of the atom of process which is an actual occasion, I feel in a quandary, for it is impossible to do this in a way which will carry conviction without going to lengths which would take me far beyond the scope of this book. My object in attempting it is to introduce the ideas which will provide for an interpretation of the living organism as a nexus of psychophysical agents responding purposively to stimuli, and in particular for the interpretation of the act of perception, a percipient event.

An actual occasion is an atom of experience or feeling. But this implies objects for it to experience. These are provided by its immediately preceding contiguous actual occasions, and through them by more remote actual occasions, and others which complete themselves during the specious present of the actual occasion in question. The nascent actual occasion is said to *prehend* the antecedent occasions, or such constituents (*aspects*) of them as are relevant to its own constitution (its subjective form). The totality of their constituents prehended by the nascent occasion constitute its *objective datum* (i.e., objects given to it for experiencing). It is clear that in the case of an enduring object, the dominant contributor to the objective datum is that actual occasion which stands to it in the special relation of predecessor-successor. Since prehension is, as we shall see, the basis of perception, it follows that the most important among the objects perceived is the percipient's own immediate past. This is an example of what Whitehead (1933, p. 233) calls non-sensuous perception. Thus our relation to our past is of the same nature as our relation to events in our bodily organs, such as the eye, which, when pre-

hended by an actual occasion in the Central Agent, are experienced by it as a member of the class of feelings known as *sensa*. This will be shown to be of great importance for an understanding of the relation of the subject which is the animal as a whole to its cells and other subjects of its body.

Since the objective datum is provided by actual occasions, and since these are themselves processes of feeling, it follows that the objects of experience for any actual occasion are feelings. An actual occasion 'feels the feelings' of the preceding actual occasions which it has prehended. The course of an actual occasion is a *concrescence*, or growing together, of feelings into a single unitary feeling which is the subject reconstituted in each specious present 'the feeler is the unity emergent from its own feelings' (1929, p. 123). The subject (the feeler) is constituted out of its objects of experience (its feelings) and in turn becomes an object of experience for succeeding actual occasions. The feelings which undergo concrescence into a subject are partly feelings already constitutive of the objective datum (and therefore feelings which were constitutive of antecedent actual occasions) and partly new feelings arising by concrescence of these feelings into new wholes.

It is in this way therefore that actual occasions become determinants of the course of the concrescence which is another actual occasion. Whitehead speaks of this aspect of the causal action of antecedent on subsequent actual occasions as the transmission of *physical feelings* from the former to the latter. 'The physical theory of the structural flow of energy has to do with the transmission of simple physical feelings from individual actuality to individual actuality.' (1929, p. 360.) 'Physical science is the science investigating spatio-temporal and quantitative characters of simple physical feelings.' (1929, p. 338.) 'A simple physical feeling is an act of causation. The actual entity which is the initial datum is the "cause," the simple physical feeling is the "effect," and the subject entertaining the simple physical feeling is the actual entity "conditioned" by the effect.' (1929, p. 334.)

The concrescence of feelings entering into the constitution of an actual occasion is conceived as a forwardly directed, teleological, process. The actual occasion is said to have *subjective aim*⁴ at the self-completion of the concrescence of its feelings into one unitary feeling, which I think can be described as a feeling of the

4. As I understand him, Whitehead considers that subjective aim is primary. The nascent actual occasion is a bare aim at self-completion. The form that this will take depends on its subjective form as inherited from its predecessor, and as modified by other components of its objective datum.

meaning of the whole experience. To an electronic occasion, if it were conscious and could introspect its own process, the meaning emerging from and guiding the concrescence would be that of becoming a particular kind of electronic occasion. But as actual occasions are not only effects of their predecessors, but are causes determining the character of their successors, to aim at becoming such an electronic occasion is to aim at being the cause of its successor having the character of an electronic occasion occupying a certain space-time location (that is to say, a member of the temporal nexus of actual occasions which constitutes an electron moving in a particular direction and with a particular velocity). To a percipient occasion in the human mind, the meaning includes the setting in train of the nexus of events which is the appropriate response to the perceived situation. The details of the process of arriving at this meaning are discussed in the next section.

This completion of the process which is the actual occasion, and which I have ventured to describe as finding the meaning of the experience, is called by Whitehead the *satisfaction* of the actual occasion. Once this is achieved, the actual occasion is over, for the subjective aim, being now satisfied, ceases to operate. But although actual occasions perish, they are said to have *objective immortality*, because their constituent feelings enter into and become part of succeeding actual occasions. Antecedent actual occasions are thus efficient causes of the character of subsequent actual occasions. But the relation is something more than that of cause and effect. The cause persists in the effect. In the nexus of actual occasions constituting a mind, this means that past experience does not merely affect present experience, but persists in the present experience.

Thus also it is seen that subjective aim is more than merely an aim of self-completion. For its satisfaction is not a terminus. Satisfaction is the completion of the actual occasion as an agent determining the course of other events. It is, however, cardinal to Whitehead's system that the determination of an actual occasion by preceding events is not complete. Something is left for determination by the occasion itself. Unless there were some selection of possibilities there would be no reason for the conception of subjective aim. It would be enough to describe an event as an effect of preceding events, and automatically becoming after an interval of time (its specious present) a cause of other events.

Subjective aim is final causation, and operates by a selection of the possible ways of integrating the components of the objective datum so as best to satisfy the subjective aim in its function, not merely of self-completion of the present event, but as a cause of appropriate subsequent events. The meaning of the objective datum has to be found; it is not given entirely automatically. The justification for this idea is the justification for all teleological as opposed to purely physical theories of the behaviour of living organisms, including man. Certainly, in the case of a physical event such as an electronic vibration, we incline to suppose, with Whitehead, that anything left over for determination within the course of the event itself must be vanishingly small, and that its course will be all but automatically determined by the objective datum. Nevertheless, if teleology is to have a place in nature anywhere, one must be sympathetic to a philosophy which finds it in principle everywhere, as we find efficient causation everywhere. Indeed, one of the difficulties in accepting teleological causation is its apparent incompatibility with physical causation. If the chain of physical causation is complete and continuous, where can we intercalate teleology into the causal series? Whitehead finds a place for it in the fact that the links in the causal chain are not instantaneous, but occupy a finite extent of space-time.⁵ Final causation is located within the event itself, physical causation at, so to speak, the junction of events. In his system, final causation is not an *ad hoc* explanation of the adaptive acts of living organisms, but a metaphysical feature of the whole of nature. In fact, strictly speaking, it is no longer possible to speak of mental as opposed to physical events, since every actual occasion has both a mental and a physical 'pole.' Its physical pole is constituted by its 'physical feelings,' transmitted to it by other actual occasions. Its mental pole is its function of finding the meaning⁶ (for it) of its prehended physical feelings.

In the first two chapters it was pointed out that if cells, and certain other living parts of the organism, have the status of

5. Cf. B. Russell (1927, p. 366): '... relativity should prepare our minds for the oddest features of the quantum theory, namely the existence of causal laws involving whole periods. The causal unit, on relativity principles, should be expected to occupy a small region of space time; it should not therefore be instantaneous as in pre-relativity dynamics.'

6. As Whitehead does not use the word 'meaning,' it seems necessary to state that his account of the mental pole is in terms, partly of subjective aim, and partly of origination of conceptual feelings of eternal objects. Eternal objects are universals or qualities—in fact, ideas, in at any rate some usages of that word. These ideas arise by virtue of their relevance both to the physical feelings and to the subjective aim of the actual occasion. For example (my own, not Whitehead's), the same nexus of visual sensa may have for me, according to my purpose at the moment, the meaning of a book to read or of a handy paperweight.

subjects, the subject which is the organism as a whole—the Central Agent—does not exist from the egg onwards but is generated by the constituent subjects at a later stage of embryonic development. We are now in a better position to give a more precise meaning to this statement. The problem of the generation of a subject is bound up with the problem of its continuance. On the views I have been attempting to expound, the generation of a subject by other subjects, and its persistence after generation, are processes of a like nature. Whitehead's system gives a new meaning to 'persistence,' to be found in his conception of an enduring object. The mind of a man is an enduring object, constituted by a temporal nexus of actual occasions, each with the duration of a psychological specious present. In each actual occasion the subject is re-constituted by the concrescence of feelings. The difference between the first actual occasion of the Central Agent in the developing embryo and its subsequent occasions is that whereas the first is a concrescence of feelings originating in the bodily agents only, all subsequent occasions are concrescences not only of these feelings but also of these with the feelings integrated in the preceding actual occasion of the Central Agent itself. At an early period of its development the embryo is a nexus of subjects, transmitting to each other feelings which are experienced as sensa. Thus the behaviour of each agent is influenced by sensa derived from its fellow agents. At a later stage in embryonic development, however, certain of these agents—the neurones in the brain—come into a peculiarly close relation with each other,⁷ so that their feelings, and through them the feelings transmitted to them by other agents in nervous connection with them, enter into a concrescence which is a subject of a higher order, the Central Agent. The first actual occasion of the Central Agent is thus born. For the first time the Central Agent appears as a feeler in the words of Whitehead already quoted, 'the feeler is the unity emergent from its own feelings.'

Once constituted, the continuity of experience of the Central Agent is due to the feeling by each actual occasion of feelings of its sub-agents, and also of the preceding actual occasion of the Central Agent itself. Thus the continuity of experience of the Central Agent is due to the fact that the subject of each specious present experiences at least part of the experience of

7. We have already suggested that the anatomical evidence of this relation may be the neurofibrils which run continuously through the network of neurones.

its predecessor, which similarly experienced experiences of its predecessor, and so on. Whitehead's system brings into one category both the constitution of the Central Agent by a nexus of spatially removed sub-agents, and its own continuity of experience. 'There is thus every reason to believe that our sense of unity with the body has the same original as our sense of unity with our immediate past of personal experience.' (1933, p. 243.) There is, however, a special sense of unity within the nexus⁸ forming the enduring object, the Central Agent, since each actual occasion of this nexus 'feels the feelings' of its predecessor as already unified in that predecessor, while the feelings transmitted from the bodily agents have to be integrated with this. In this process there is extensive elimination of feelings incompatible with the concrescence. This is illustrated by the fact that we only perceive objects that are relevant to our interests at the moment, or which force themselves upon our notice for some special reason, such as a peculiar intensity of the sensum. It is also illustrated in another way. In visual perception it is scarcely possible to detect the action of the receptor agents in the eye. Everything is eliminated from their contribution to the objective datum for the Central Agent except those of their feelings which are due to their prehension of the light-waves. Consequently we appear to see the object directly, not through the mediation of the rods and cones of the retina. In pain perception, however, we do have a much more direct feeling of the experience of the bodily agent concerned.

In ordinary physiological doctrine, a pain in the finger is conceived as due to a purely physical stimulus travelling from the finger to the brain, where it somehow, in a manner which it is not the business of physiology to explain, gives rise to the subjective feeling of pain. This is then referred to the place of origin of the stimulus, the finger. What is the advantage of replacing this description by the view that the feeling itself originates in the finger and is transmitted to, and re-felt by, the Central Agent? Leaving aside the metaphysical arguments of Whitehead, the answer, as already indicated, is that by so doing we place in the same category the continuity of experience of the conscious self and the continuity between the processes in the parts of the body, which for reasons already given must be considered to be feeling

8. This nexus of events corresponds functionally to Whitehead's 'nexus of presiding occasions.'

subjects also. We know that in memory we are experiencing again (though not in their completeness) experiences which we had before.

It seems in accordance with the known anatomical and functional relations of the nervous system to conclude that the relation between present and past processes in the neurones of the brain is fundamentally the same as the relation between their present processes and what happened a moment ago in the pain receptors in the finger.

It is scarcely necessary to add that it will not do to let the feeling originate in the finger and leave it there. It must be transmitted from its place of origin to the brain, and be re-felt there, for injuries to the finger which are normally followed by consciously felt pain are not so followed if the connecting nerve has been severed. The fact that mechanical stimulation of the sensory nerve itself may be felt by the Central Agent in the same way as stimulation of the receptor, may be due to the fact that the whole sensory unit from receptor to brain termination forms such an intimate nexus (perhaps on Weiss' principle of modulation described below) that any stimulus which can be prehended by any part of the nexus is felt and transmitted in the same way.

We conclude therefore that the pain felt by the Central Agent is a feeling felt a moment ago by receptors in the finger, as the feeling I am now recalling in memory was felt by a previous actual occasion of the Central Agent. It is thus that we feel it equally correct to speak of the finger as my finger and as part of me, whereas the pen in my hand is only *my* pen.

Although we have just been dealing with transmission of feelings between agents constituting the special nexus which is the nervous system, the general theory of the constitution and mutual relations of events demands that this transmission take place between all events. The type of connection between neurones, however, makes possible the prehension by the recipient actual occasion of the activities of the originating actual occasions in a more integrated form; there is a more nearly, though still far from fully, complete re-feeling of the total integrated experience of the originating actual occasions than is possible through other media than nervous connection.

I have introduced this very brief exposition of such parts of Whitehead's system as are most closely relevant to the task we

have in hand, as a possible, self-consistent, account of the body-mind relation; of the relation of efficient to final causation; and of the relation of the continuity we find in nature to the atomic character of natural processes. Moreover, his system is, so far as I know, the only system which can be applied to deal adequately with the consequences of the hypothesis (which seems inescapable) that not only the animal as a whole but also its constituent parts have the status of subjects, and that these subjects precede in time the subject which is the animal as a whole, and indeed, generate that subject.

3. *A percipient event*

In this section we shall be concerned with events in the Central Agent in their function of sensory perception. We can therefore speak of them as percipient events, remembering that in most cases we are dealing with the limiting class of events, actual occasions.

Whitehead defines his use of the words 'prehension' and 'perception' as follows: 'I will use the word prehension for *uncognitive apprehension*; by this I mean *apprehension* which may or may not be cognitive.' 'Perception is simply the cognition of prehensive unification; or more shortly, perception is cognition of prehension.' (1926, pp. 101, 104.) Prehension is therefore the more general term of the two. All perception involves prehension, but every prehension does not necessarily involve perception. For instance, the whole of the nexus of events constituting the psychophysical field is prehended in each act of perception, but only a minute portion of the constituent events are directly involved in the conscious perception. The constituents of the field of which we have cognition of prehension (and therefore perceive) are those which are discriminated from the total nexus prehended. I will use the word perception in regard to these discriminated items of the total prehended objective datum, without prejudice of the question whether they are consciously discriminated or not. The application of the notion of consciousness is full of pit-falls, and is discussed later. Moreover, although we will deal specifically with an act of visual perception, in which there is reference to an external object, I will also use the word perception for the prehension of all discriminated sensa—and, indeed, of all happenings in the psychophysical field which are experienced as having meaning or significance for the organism.

We shall use the term psychophysical field for this nexus of events which owe their origin, maintenance and modifications to bodily processes, and which is prehended as objective datum by the percipient event. This term has of course intimate association with Gestalt psychology, and indeed corresponds to its use of it in many respects, though we conceive its causal relation to mental processes very differently. Nevertheless it seems permissible to employ this term, which is too useful to be reserved for the special use which Gestalt psychologists have made of it.

We are now concerned with two main constituents of the psychophysical field, which we will call the sensory and motor *dispositions*. The sensory dispositions are those persistent features of the psychophysical field by virtue of which visual, auditory, pain, etc., sensa are possible. They must be regarded as the contributions to the field by the vital processes of the sensory neurones in the brain—or rather, through them of the specific form of activity of the whole sensory unit, under which are included the receptor cell, the afferent nerve and the terminal neurones in the brain. This activity is not solely the propagation of nerve impulses, but must be also a specific vital process continuous along the whole sensory unit. When the normal activity of a group of receptors is changed by stimulation, a correlated alteration in the psychophysical field takes place, which is discriminated as a sensum from the total background of continuous activity of the field. The change in the activity of the receptors by stimulation is transmitted very rapidly along the sensory unit in a form detectable by physical instruments as nerve impulses.

Dispositions as generally used in psychology mean tendencies to certain specific forms of conscious experience, for instance specific visual images due to past experience, or in the case of instinctive behaviour, to innate features of the organism. Such dispositions may be referred to as a visual disposition, or a motor disposition, in distinction from the general visual disposition and motor disposition.

Similarly, motor dispositions are those persistent constituents of the psychophysical field by virtue of which effector actions are possible. Again, they are not maintained by nerve impulses—indeed they could not be, since these are centrifugal in the motor nerves. They must be maintained by centripetal transmission from the effectors to the psychophysical field. As I shall argue

from a consideration of the processes involved in perception, it is not possible to regard the Central Agent as having only a one-way connection with its receptor and effector agents, being concerned only with incoming processes from the former and with outgoing processes to the latter, as assumed in the telephone exchange analogy of the function of the brain. On the physiological side, a possible basis for centripetal transmission from effectors to the psychophysical field is, it will be suggested, provided by Weiss' conception of 'modulation,' to be discussed later.

Since the function of the sensory and motor dispositions is essential to an understanding of perception, it is necessary to introduce here a rather long digression from our description of a percipient event in order to examine the nature of these dispositions in more detail. This will involve an elaboration of the views already outlined as to the nature of the relation between the agents of the body.

Let us introduce the discussion by reference to the thesis developed by Allen (1930). He points out that all bodily organs must normally be in a state of activity specific for that organ. This is illustrated in muscle tonus, for example, but must be extended to receptor organs and their afferent nerves. To all these organs, as to all living agents, the affective tone of normal functioning is pleasure, in its most general sense as opposed to unpleasure. But the low state of activity in which receptors and their nerves persist while not stimulated is, if long continued, insufficient to maintain this state of pleasure. There is a 'craving' on the part of the organ for fuller activity, which can only be obtained in the form of response to stimulation. This craving may or may not be consciously experienced by the Central Agent. But when it is not so experienced, it must be present as a potential object of experience—in other words, as a feature of the sensory disposition under these conditions (remaining in the sub-conscious in Allen's terminology). This can be deduced from an examination of sensory experience. Consider for example the experience of a sweet taste. This experience is not pleasant under all circumstances. If we have recently been sated with sweet things the taste becomes positively unpleasant. This is because the continued stimulation of the sensory unit (which includes the receptor, the afferent nerve, and the brain centre) has caused in it an excessive and damaging activity. The craving of the sensory unit for activity

has been oversatisfied, and its normal or optimum state can only be restored by a period of the low activity which persists in the absence of specific stimulation. On the other hand, the pleasure one obtains from an occasional chocolate consists, as Allen says, in the feeling 'That gives me something I was just wanting.' We were not conscious of a desire for something sweet, but our pleasure in it discloses the fact that there was such a subconscious desire. This subconscious desire may also be brought into consciousness by the mere sight of the chocolate. If we have been deprived of sweet things for a long time, we may even have a conscious craving for something sweet, without anything to suggest it except the strong craving for functioning on the part of the sensory unit itself. Thus sensory pleasure is caused by normal functioning of the bodily organs; for this, moderate periodic stimulation is necessary. Sensory unpleasure may be due to under-stimulation causing prolonged insufficient activity on the part of the sensory unit, or in a more acute form by over-stimulation causing a fatiguing or damaging excess of activity.

This conception of a craving or conation for normal functioning by the organs themselves, and not merely by the Central Agent, explains also why the mere idea of a sweet taste is not itself satisfying, as it surely should be if the desire for something sweet was itself an idea originating in the Central Agent. The fact that the desire can only be satisfied by stimulation of the appropriate receptors shows that the desire originated in them.⁹

The sense of taste affords a particularly convincing argument for this thesis, but Allen applies it also to the other senses. For instance, undue stimulation of the visual and auditory sensory units by excessive light and violent noises is unpleasant, while prolonged complete darkness or silence are felt as oppressive. He gives evidence that though it may seem paradoxical to speak of a consciousness of a craving of the pain nerves for stimulation, a very mild stimulation of these is actually pleasant, though in their case the point of over-stimulation is reached much earlier than in other nerves.

Thus the activity of the receptor cells is not merely transmitted as a physical stimulus through a chain of neurones to the brain, where it somehow generates a feeling, but the feelings of the

9. On the other hand, ideas originating in the Central Agent are satisfied by other ideas originating in that Agent. The desire for a solution of the problem why the imagination of a sweet taste does not satisfy a craving for a sweet taste is satisfied by another idea, the one we have just expounded, namely, that the craving originated in the sensory unit and therefore can only be satisfied in the sensory unit.

receptor (that is, the receptor's feelings) are themselves transmitted. The Central Agent 'feels the feelings' of its receptor cells. Moreover, we have to conclude that the relation between the receptors and the Central Agent is not primarily maintained by the passage of nerve impulses, but by the transmission of continuous vital processes along the sensory unit. Nerve impulses, on this view, are a specific change or enhancement of this continuous transmission, a conception made familiar by the work of Child on the axial gradient of metabolic activity (chapter v).

Turning now from sensory units we may consider Weiss' (1936) experiments and conclusions on the interrelation of the constituents of a motor unit. This is the term given by Sherrington to a single motor neurone and the bundle of muscle fibres it innervates.

Weiss transplanted the limbs of amphibian larvae in a number of ways, including the interchange of right and left forelimbs, and the establishment of supernumerary forelimbs by transplanting an additional forelimb from another larva in the neighbourhood of the forelimb of the host. At the time of the operation, a branch of the brachial nerve plexus was cut, so as to allow of the outgrowth of nerve fibres from it. The original motor nerves in the transplanted limb, being severed from their ganglion cells, degenerate and are replaced by the new nerve fibres growing out from the cut nerve of the host. Until these nerve fibres have made connection with the muscles, the limb is, of course, paralysed. Some weeks after transplantation the new supply of nerves is established and the limb becomes fully functional in its new position.

The significant fact about this functioning is that muscular action is always homologous in the original and transplanted limbs; for example, both are flexed or both are extended together, whether the transplanted limb is orientated in its proper way or not. If a supernumerary forelimb has been produced by transplanting the right limb of another animal on to the left side of the host, so that the two forelimbs of the left side are in the relation of mirror images to each other, then a forward stroke of the one is accompanied by a backward stroke of the other; the two actions cancel each other so far as their effectiveness for swimming or walking is concerned. If the right and left forelimbs of the same animal are interchanged, so that the elbow joints of both limbs project forwards instead of backwards, when the animal intends to walk

forward, the forelimbs actually move it backwards. 'This type of functioning, perfectly absurd from the standpoint of the body, has never ceased nor even changed during the several months of observation, extended beyond the metamorphosis of the animals.'

Weiss used fully differentiated and functional limbs for transplantation. Similar results have been obtained by other workers using transplants of undifferentiated embryonic limb rudiments.

This homologous action of the limbs applies not only to the limbs as wholes, but also to the individual muscles. When the triceps of one limb contracts, so does the triceps of the other, and so on for all the separate muscles. Weiss concludes that this indicates that the 'commands' issuing from the motor centres in the spinal cord are not for thrust, flexion, grasp, or the like, but are already fragmented in the motor centres into calls for individual muscles to participate in the movement.

From a number of experiments designed to test alternative hypotheses, Weiss draws very important conclusions about the way in which the individual muscles in the transplanted limbs gain their relation to the motor centres. At first, the transplant is devoid of nervous connection with its host. In the process of obtaining this connection by means of the outgrowth of nerves from the host, there is no specific attraction by the individual muscles of specific nerve fibres which have grown out from corresponding nerve cells in the motor centres of the host. The nerves grow out from the host into the transplanted limb, and there make connection with the muscles, in quite unspecific fashion. (This conclusion is based upon convincing evidence.) Weiss concludes that after the nerve fibres have become connected to the various muscles, each separate muscle exerts a 'modulating' influence, specific for that muscle, on the nerve fibre connected with it. This modulation extends right up the fibre into the nerve cell in the spinal cord, so that the whole neurone becomes modulated in conformity with the particular muscle with which it is connected. Modulation consists in rendering the motor unit¹⁰ insensitive to all qualities of nerve discharge but one. The motor neurones in the motor centres are in interplay with a central system (Weiss' 'central action system') from which each motor

10. By Sherrington's definition, a motor unit is a single motor neurone and the bunch of muscle fibres which it serves. Each muscle is, however, made up of a number of such bunches of fibres, and is therefore served by a group or 'pool' of motor neurones, the cell bodies of which are situated in the spinal centre. For example, the pool consists of about 480 neurones in the case of the muscle which flexes the knee joint of the cat. Since, however, an entire muscle is evidently the modulating unit, we must suppose that the whole assembly of motor neurones serving a particular muscle undergoes similar modulation.

neurone picks up selectively its proper component. It is to be noted that this conception could be extended to supply the physical conditions demanded by Lashley's conclusion that motor paths become sensitized to a 'pattern of excitation' so that they will respond to this pattern in whatsoever part of the nervous tissue it may occur.

We must note also a further conclusion drawn by Weiss, which is important to the conception of the body as a nexus of living agents. He points out that it is no longer possible to look upon the muscular system as a mere mass of flesh cast into elements, the functioning of which is to be interpreted solely in terms of its appropriateness to bodily movements. On the contrary, the muscular system is composed of as many discrete and distinct individualities as there are non-homologous muscles, each possessing certain personal characteristics prevailing over all such concerns as anatomical arrangement or functional significance.

It is of course well known that the higher animals can learn to make their muscles function in ways incompatible with their normal relation to their motor centres. The lack of educability in the Amphibia in respect to muscular action revealed by Weiss' experiments contrasts with the educability exhibited by the higher animals and man. In the Amphibia studied by Weiss, the reversed forelimbs continued to the end to function in their original way, contrary to the needs of the animal, while in the higher animals muscles which have been artificially connected to a foreign nerve are soon made to function so as to bring about the movements desired by the animal. Weiss attributes this difference between the Amphibia and the higher animals to the fact that whereas in both cases the phenomenon of homologous response is due to properties of the spinal motor centres, in the higher animals there is greater cerebral control of these centres.

I have introduced this conception of Weiss' because it may be used to bring the relation of the Central Agent to its effectors into line with its relation to its receptors, in spite of the fact that in the motor nerves the impulses travel from the brain to the muscles and not in the opposite direction. Perception involves, or often involves, finding the meaning of sensa in terms of action, and as will be argued later, this implies the potentiality of imagining or feeling (or rather pre-feeling) the performance of an action which is not actually in progress. This potentiality cannot be fully accounted for by memory images of past actions,

since the meaning of sensa in terms of appropriate action can be found in instinctive behaviour without relevant previous experience. A basis for it is provided by the 'modulation' of the vital processes of motor units spreading up from the muscle to the central neurones in the brain. Thus the motor disposition of the psychophysical field contains components which are similar to those of the sensory disposition which are the basis of sensa. When discriminated from the total motor disposition, these components can be integrated with sensa, giving the meaning of the sensa in terms of action, just as on the cognitive side visual, auditory, and other sensa, are integrated into the cognition of an external object.

Each occasion or event of the Central Agent therefore prehends not only its own predecessor, thus continuing its experience, but also the modifications of the psychophysical field effected during its specious present by transmission from its bodily sub-agents. By prehending these modifications it is not merely causally affected by them in some way, but through them it 'feels the feelings' of the receptor and effector organs. By prehending them the Central Agent continues in itself their feelings, just as it continues its own past experience.

This notion can perhaps be helped out by the analogy of a river, fed by numerous tributaries. The main stream represents the Central Agent, and its flow in space is the flow in time of the experience of the Central Agent. The tributaries entering the river along its course are the flow of feelings transmitted to the Central Agent through the psychophysical field from other bodily agents. On entering the river, the tributaries are merged into it, and the continuity of the river now extends back not only along its own main stream but to the source of each tributary which it has received up to that point. The relation of any part of the river to the earlier parts of its own main stream is the same as its relation to the tributaries that have already entered it. Similarly, the Central Agent's own previous experiences (the main stream) and the experiences of its sub-agents (the tributaries) enter into its present experience in identical fashion. The entry of the tributaries into the river is the analogue of the Central Agent's feeling the feelings of its sub-agents, ultimately of its individual cells.

The continuity of experience of the Central Agent which gives

it continuing personality is therefore not merely a continuity of its own experience in the narrow sense of the word 'own.' It is not merely a continuity of the occasions of experience which constitute the temporal nexus of events which is the Central Agent proper. The experience of the Central Agent incorporates the feelings of the bodily organs, prehended by it through the psychophysical field. Similarly, each element or cell of a sensory or motor unit is not merely thrown into a state of excitation by the activity of its contiguous elements, but likewise continues the feelings of these elements in itself. We may again remind the reader that to Whitehead the flow of energy is the transmission of feelings ('simple physical feelings') from event to event, by virtue of which each actual occasion in prehending its predecessors continues the feelings entertained by them. Thus the community of feeling within the members of a nexus will also be a community of physical processes, transmitted from one member to another. A special example of this is Weiss' process of modulation.

I have used the terms sensory and motor units as defined by Allen and Sherrington respectively, but it is clear that the activities of these units are not prehended by the Central Agent as units, but as already integrated into nexus. All sensory nerve fibres have passed through lower co-ordinating centres before they reach the cortex. The motor units are already combined into nexus in the spinal cord and into more comprehensive nexus on their way to, and in, the cortex. We do not feel or imagine the movement of individual muscles, still less of the bundles of muscle fibres within a muscle activated by a single motor neurone. We feel and imagine movements brought about by co-ordinated action of numbers of muscles. Wherever motor and sensory units are referred to, it is therefore to be understood that no functional independence of the units or of their parts is implied.

When we say that one agent feels the feelings of the other agents which act upon it, we do not mean that the quality of the feelings necessarily remains the same, for each agent prehends the feelings of the others in a nexus containing other feelings, including those of its own proper processes. The most exact reproduction of feelings in the Central Agent is of the feelings in its own antecedent occasions, which may be prehended very nearly in the form in which they were integrated in those occasions. This is illustrated by memories. The prehension by the Central Agent of the feelings in its bodily sub-agents (in the form of *sensa*) must

be attended by much elimination from the totality of their feelings. For instance, in the perception of redness, what we are conscious of is not the totality of feelings in the receptor cells of the retina, but only that part of their feelings which makes the difference between the sensa of redness and of any other colour. (As in discussion with another man, we pay attention to his opinions on the subject under discussion but ignore innumerable other aspects of his personality.) If we are to follow Whitehead whole-heartedly, we must not, however, stop at the surface of the body. Since in his system all causal transmission—even what seems purely physical transmission—is transmission of feelings, the visual receptors also 'feel the feelings' in the thing seen. How far the feelings felt by the rods and cones are the 'same' feelings as those in the things seen could, however, only be discussed on the metaphysical plane, and it is not part of our programme to follow up the implication of Whitehead's system outside the world of living organisms.¹¹

We must now return to the analysis of the act of perception. The sensory disposition of the psychophysical field is the nexus of activity of the central neurones of the sensory units. The motor disposition is the nexus of activity of the central neurones of the motor units. Specific changes in the sensory disposition, produced by changes in the processes of the sense receptors, are experienced by the Central Agent as sensa. As we have seen, the motor disposition contains components—the activity of groups of specific motor neurones—which have the same relation to specific organizations of muscles as the components of the sensory disposition which are the basis of sensa have to receptor organs. Whereas sensa, however, owe their discrimination from the total background of activity of the sensory disposition to peripheral stimulation of receptors, components of the motor disposition become discriminated from the total activity of the motor disposition by forces in the psychophysical field itself. This happens in every act of perception where the meaning of a sensum is in terms of action. These discriminated components of the motor disposition are experienced in a mode for which the term 'imagined action' suggests itself, in analogy with centrally aroused imagined sensory experience (as

11. The reader may be referred to Hartshorne for a systematic development of a theory of the philosophy and psychology of sensation on the basis that the cells of the body are sentient and feel each other's feelings, together with other consequences of a theory of feeling similar to Whitehead's and leading to pansychism.

when we imagine the sight of an object without actually seeing it). The word 'imagined' carries with it, however, unnecessary implications. The experience can better be described as a pre-feeling of the corresponding action, or better still, as the anticipation of the action about to be performed. I shall call these anticipated actions *conceptual actions*.¹² If we grant that the acts of organisms are directed to ends, it seems necessary to assume that the overt action which is the response to a sensum is always preceded by conceptual action, for the end, even if it is to be achieved by a single muscular or protoplasmic movement, is in the future, while the efficient cause of the action must be in the present.

As was stressed in chapter 1, perception is primitively experience of something causally affecting the percipient, with anticipated consequences and therefore conceptual action relevant to these consequences. The quality of the anticipated experience is its affective or emotional tone. The most primitive forms of affective tone are probably pleasure and unpleasure, or well-being and discomfort, and the sensa areprehended as meaning whatever action is available to the organism for continuing or altering the present affective tone. The higher forms of perception may be derived from this by elaboration of the sensory and motor dispositions, which in turn depends upon the elaboration of receptor and effector organs or agents. Thus the primitive affective tones of pleasure and unpleasure differentiate into the specific emotions of fear, anger, sexual emotion and the like. For meaning can only be given to sensa in terms of actions actually available to the organism.

A sensum experienced with the affective tone of fear¹³ evokes

12. In Whiteheadian terminology this would be, I think, 'a conceptual feeling of a specific action.' This 'pre-felt' action is not to be confused with the feeling of the action while this is in progress, which is mainly due to sensory impulses received during the movement from the skin, and especially from sense receptors embedded in the muscles themselves, which are stimulated by tension and relaxation of the muscles. This is illustrated by the diminished control over the movements of the limbs in locomotor ataxia, which is due to degeneration of the sensory nerve fibres. Mott and Sherrington found, however, that volitional movements of the arm and leg in monkeys were not completely abolished by section of the dorsal roots of the appropriate spinal nerves, thus depriving the monkey of all sensation from the operated limb. Moreover, human patients in whom an arm has become insentient through disease can institute voluntary action by it, though the action proceeds clumsily. This seems to show that the possibility of conceptual action depends on the motor as well as on the sensory components of the psychophysical field; the distinction between sensory and motor dispositions, as between the sensory and motor units within their respective dispositions, is indeed only relative, as in the case of all interacting nexus.

13. The well known James-Lange theory of emotion ascribes emotional feeling to a feeling of visceral changes produced as the effector consequences of the percipient event. According to this theory, the feeling of fear, anger, and so forth is not a feature of the mode of prehension of the visual, auditory or tactile sensum, but is associated with it owing to the feelings of visceral changes following the act of perception. Sherrington, however (1920, pp. 260-266), has shown that a dog which by appropriate transection of the spinal cord and vagus nerves has been deprived of all visceral sensations still shows, without obvious diminution, all the normal signs of anger, joy and fear. From this, and other experimental

the discrimination from the total motor disposition of a specific motor disposition experienced as anticipated escape action; indeed, the anticipation of escape action possibly *is* the affective tone. In a simply organized animal with only one possible mode of escape action (such as withdrawal) there is only one possible motor disposition relevant to escape; this, therefore, necessarily becomes the conceptual action which is the conative element of that act of perception. In a more complexly organized animal, however, there are many possible variants of the escape action, only one of which is to be selected.

Probably on any theory of behaviour, certain general features of the relevance¹⁴ of sensa to action, that is to say, their affective tone, must be taken to be inescapably given in persistent features of the psychophysical field. But it is a cardinal feature of adaptive behaviour that the relevant action is only thus given in a general way, and that the particular action has to be suited to the particular circumstances of the total perceived situation. Any really adaptive behaviour involves anticipation of possible experiences, and selection of action to avoid or realize these experiences. But the actions themselves are in the future, and what has to be selected must be in the present. There must be a selection from real possibilities of action, and these possibilities are the conceptual actions. The anticipation of future experiences which we know in ourselves, and can confidently infer from the behaviour of animals, would have no function to perform if we were powerless to act in accordance with that anticipation. If there is not a real selection of possibilities of action in respect to the anticipated experience; if the action is completely determined by the nature of the stimulus, innate organization and past experience; then men and animals have simply to take what is coming to them, and their capacity of anticipating what this is to be before it comes, is a capacity which has no function to perform. We must conclude, therefore, that in all adaptive action there is a real selection of possibilities of action.

facts, he concludes that the visceral reactions are not the excitants of emotion, though they strengthen it, and contribute to the energy of the behaviour. Cannon has also cited experimental evidence that in animals emotional behaviour, and in man emotional feeling, are not dependent on visceral changes. We may add that organic conditions existing prior to the percipient event may predispose the Central Agent toprehend a sensum with a specific emotional tone, as illustrated by the different responses of an animal to a sexual sensum when its sexual organs are in different physiological states.

14. While relevance (or meaning) as such must be taken, on the plane of this discussion at any rate, as an ultimate fact, specific relevances of sensa to conceptual actions are the result either of the evolutionary process when they are innate, or of previous experience of the consequences of sensa when they have been learnt.

This of course involves a comparison and judgment between the possibilities. That this is so in every act of perception, even when overt action is not involved, seems clear. When I perceive a cat, the fact that I see it is a cat implies that I see that it is not a dog. Among the various animals it might be, I have decided (without conscious deliberation) that it is this sort of animal and not that sort. When overt action is involved, a judgment between alternative actions is also implied. The fact that I see an angry dog as an object to be avoided implies that other actions towards it are possible and have been rejected. The completion or 'satisfaction' of the actual occasion which is the percipient event partakes therefore of the nature of a decision in Whitehead's sense—the cutting off of all possibilities but one.

To sum up: the temporal endurance of the Central Agent, like that of any other enduring object, is made up of a succession of periodic processes, its actual occasions, exhibiting a continuity of character due to the relation between successive actual occasions already discussed. In simpler enduring objects, such as molecules and electrons, each actual occasion is virtually a repetition of its predecessor. The Central Agent, however, is constituted in the first instance, and subsequently influenced, by concrescence of feelings transmitted from the bodily sub-agents to the brain neurones, whose nexus of activities constitute the psychophysical field. Hence the course of successive actual occasions of the Central Agent are profoundly modified by changes in the bodily sub-agents transmitted to the psychophysical field as feelings of the class known as *sensa*. The actual occasion, in its character as an act of sensory perception, is a concrescence of these *sensa* with other relevant constituents of the nexus of feelings constituting the psychophysical field as organized by preceding actual occasions. These constituents are (1) those due to relevant past experience, (2) conceptual actions discriminated, by virtue of their relevance to the *sensa*, from the total nexus of potential conceptual actions represented by the motor disposition of the psychophysical field. The meaning of the *sensa* is thus established. This is the 'satisfaction' of the actual occasion and appears physically (in part) as the transmission of energy to those motor neurones, the nexus of whose feelings provides the conceptual action in question. These motor neurones, which are themselves living agents, prehend this as a *sensum*, which has for them a meaning which appears physically as the initiation of a nerve impulse.

4. Consciousness

The interpretation of living organisms as feeling and perceiving subjects, as nexus of subjects, and as purposive agents, inevitably raises the question whether they must therefore be conscious. We must not, however, let our discussion of this take the form of denying feeling, perception and purposive action to organisms unless we have first decided they are conscious. We must accept their feeling, perceiving and purposing, and discuss whether this necessarily implies that the organisms are conscious. The discussion will help to make more explicit the grades of complexity which are to be found in living organisms, but it is not important for our general thesis to come to any conclusion about their consciousness except in relation to evolution. It makes no difference to our argument whether we hold with some philosophers that consciousness is the hall-mark of a mental process, or with others that it is a feature of only a limited class of such processes. The belief that the lowest living organisms are not conscious would, however, affect our views on the process of evolution, for we know that at least one of the higher organisms is conscious. Are we to assume that human consciousness is a more developed form of something characterizing all living organisms, or has consciousness 'emerged' at some point in the evolutionary process? The same problem arises in the relation between living organisms and inanimate or physical processes. As we have seen, Whitehead finds a fundamental identity of metaphysical structure in the elementary events, the actual occasions, of all process, including both mental and physical in the ordinary usage of these words. He, however, is quite explicit that consciousness should not be attributed to the simpler types of actual occasions. Although the process of every actual occasion is directed to an end, its subjective aim, only a small class of actual occasions is of the conscious form. Thus (1929, p. 72) : 'The principle I am adopting is that consciousness pre-supposes experience, and not experience consciousness. It is a special element in the subjective form of some feelings. Thus an actual entity (occasion) may or may not be conscious of some part of its experience. Its experience is its complete formal constitution, including its consciousness, if any.' Emmet (p. 115) says: 'Whitehead would say that consciousness emerges with the explicit recognition of alternatives—e.g., that A is black, and not white. But purpose, valuation and "subjective aim" are far more primary than consciousness.'

According to Whitehead, therefore, there was a date in the history of the world on which consciousness first appeared. Moreover, his view seems to allow only a minor function to consciousness. It enables something to be done better than it could have been done without it. No doubt the choice between this and the alternative, that consciousness has always been present, is a matter of prejudice or taste, incapable of convincing argument either way. To many, the more satisfying hypothesis is that all process (in Whitehead's sense) is of the nature of experience, and—contrary to Whitehead—that all experience is in its degree conscious. If this is so, we must ascribe consciousness to every living agent, such as a plant cell or a bacterium, and even (if the continuity of nature is not to be broken) to an electron. Since, however, we are primarily concerned with living organisms, we need not extend our discussion beyond them.

One of the reasons for a certain reluctance to attribute consciousness to a tissue cell or to a bacterium is that many things which we do, apparently without being conscious of doing them, are so much more complicated than anything which these lowly organisms can do that it seems unnecessary to suppose that their simple responses involve consciousness. The problem of the apparently unconscious reflexes of the higher organisms has already been touched on in chapter 1, where it was pointed out that, on the view that a higher organism is a nexus of agents, a reflex action does not, or need not, involve the Central Agent at all. Any consciousness accompanying the action would therefore not be consciousness on the part of the Central Agent, but of agents of a lower order. Moreover, there are many actions which may be reflex on most occasions but consciously controlled on others; for instance, walking, or the fixation of the eyes on the object we are looking at. It may be that these actions are normally controlled by subordinate centres of integration (subjects of a lower order than the Central Agent) whose activities do not normally form discriminable constituents of the objective datum for an occasion of the Central Agent, though under special circumstances they may do so. Possibly some of the operations of the 'unconscious mind' are to be explained in the same way, especially those which must involve trains of thinking of which we know nothing until their final product isprehended by the Central Agent as the solution of a forgotten problem. It may be that the operative subject here is one of the higher sub-agents in

the hierarchy between individual cells and the Central Agent; sub-agents which may have no recognizable anatomical boundaries and which may form enduring objects of only limited duration. These speculations, however, are immaterial to our general thesis, which does not depend upon the activity of the mental pole of an actual occasion being accompanied by consciousness. It must be remembered also that there are many complex organisms where there is no evidence of a Central Agent. For instance, all plants, and sponges among animals. In these 'living democracies' (Whitehead) there can be no consciousness attributable to the organism as a whole, but only a multitude of separate consciousnesses.

This, however, does not entirely dispose of the argument from our own apparently unconscious actions, for actions which, we must suppose, involve the Central Agent are also constantly occurring without apparent consciousness.

To be conscious is to be conscious of something. A self-conscious being is conscious of being conscious. An organism is, however, conceivable in which no experience, after it had passed into the nexus which is the psychophysical field of the Central Agent, could become discriminated from the general nexus; that is to say, no past experience could become an object of experience, or remembered. Such an organism might at each moment consciously feel pain,¹⁵ pay attention to objects, and be aware of the ends to which each present action is directed, and yet never know that it was conscious of doing these things, because when it started to introspect, the process which was to be the object of the introspection would already be in the past and not discriminable from the general body of past experience.¹⁶ If it asked itself, am I feeling pain? before it could be answered the question would already be in the past and therefore forgotten. It appears that in order

15. Cf. Price (p. 121). ' . . . every phase of the process (of human feeling) is accompanied by awareness of the previous phases; and though in a process A B C, the fact that B is accompanied by the awareness of B makes no essential difference to it, yet the fact that B is accompanied by the awareness of A may very well make an essential difference. . . . Every phase of the process is coloured with or includes as an essential part an awareness of the previous phases, and of the fact that they inhered in the same self that is now aware of them. This "snowball-like" character of including within itself the awareness of its own past is what distinguishes felt fear, for instance, from unfelt or unconscious fear, and distinguishes them so sharply that the word "fear" can only be applied to the second in an equivocal or at best an analogical sense.' Thus Price would call a process of feeling which is unaware of its own past an unconscious feeling. Obviously, there is no means of discovery whether it was, at the moment, conscious or not, and as stated above, a decision on this matter is not important for our purposes except from the evolutionary point of view.

16. A form of self-consciousness more fundamental than that depending on the capacity for introspection must be recognized. This is what Bowman (p. 260) calls primary self-consciousness, and is implied by the fact of consciousness itself. For it is impossible to be conscious and not at the same time experience the self as the subject concerned. The mode of self-consciousness which we are discussing is the reflective or introspective mode, which Bowman calls secondary self-consciousness, dependent on, and derivable from, primary self-consciousness.

that a single item of past experience, even if conscious at the time, can become discriminated from the total body of past experience it must have had a certain minimum intensity of consciousness, or be rescued from obscurity owing to its relevance to some other experience which possesses the necessary intensity (the psychological principle of association). A conscious, but not self-conscious, organism might owe its lack of self-consciousness either to low intensity of consciousness in the original experience, or to the fact that the constitution of the psychophysical field did not allow those constituents of it which are due to past experience to become objects of experience in subsequent actual occasions in the Central Agent. The organism would not be self-conscious, for consciousness of self is consciousness of a stream of past experiences recognized as belonging to that self.

Such an organism would be permanently in the position in respect to the totality of its past experiences that we ourselves are to many, or even most, of our own experiences. Innumerable perceptions, thoughts and actions can never become discriminated in a subsequent mental process. We perceive many things without paying sufficient attention; that is to say, with such a low degree of consciousness, that immediately afterwards we have no direct knowledge that we perceived them. Nevertheless, we can be confident that we do perform these acts of perceiving, for two reasons. First, because although we have forgotten the fact that we perceived them, the fact may be brought to light subsequently by association with some later perception or idea. Second, because we are aware of grades of attention in our acts of perceiving. If while I am absorbed in my work the clock strikes, and a few seconds later someone asks me if I heard it strike, I answer yes. But if a minute or two has elapsed between the clock striking and the question, I shall answer no. Such acts of perception, though conscious at the time, remain discriminable from the total nexus only for a very short time.

The limiting case is that of an organism in which, though the concrecence which is the actual occasion at each specious present is a conscious process, it could never become an object of experience in subsequent actual occasions. This does not mean that its present experience is not different from what it would have been if its past experience had been different, for its sensa are prehended into a different nexus. As psychoanalysis has shown in such detail, our emotional attitude may be influenced by past events of which we have no recollection. It is true that in many

cases these can become discriminated, or brought to mind by special means; the practice of psychoanalysis consists in the attempt to do this. There is no reason to suppose, however, that those which not merely are not, but which cannot, be brought to mind do not influence us in the same way.

5. *Subjective aim and purpose*

There remains to be considered the relation between the subjective aim of a percipient event, and the purposes of human beings. The end in view of an actual occasion, its subjective aim, is to unify its prehended feelings into one determinate feeling by which it becomes the efficient cause of other events relevant to its present experience. What is usually meant by a purpose, however, is an end in view which can only be reached by a series of acts, all the members of which are influenced by the purpose. Such a purpose is an enduring feature of the objective datum prehended by the series of events constituting that stretch of the nexus between the origin of the purpose and its fulfilment. The causal efficacy of the purpose is to be found in the subjective aim of each percipient event, which prehends the purpose as it prehends its sensa or other objects of experience. The meaning of the sensa which it prehends has to be found in relation to the prehended purpose. Thus purpose operates in the same way as past experience. If a child has once been attacked by a dog, the sight of a dog will for a long time have the emotional tone of fear, which expresses the fact that it is related to, or associated with, the conceptual action of avoidance. If I have conceived the purpose of smoking a cigarette, visual sensa prehended by the succeeding percipient events will be prehended in a nexus which includes the purpose. The packet of cigarettes and the box of matches are perceived as meaning a different sort of action than they would have meant if my purpose had been to tidy my table.

Thus purpose becomes causally effective through the subjective aim of individual percipient events. Final causation is to be found in the subjective aim of actual occasions acting as efficient causes of other events relevant to their present experience.

As already discussed, the anticipations inherent in perception imply purposive action directed towards the anticipated event. Like purpose, anticipations may have a short or long range. The limiting case of short range anticipation is expressed in the effective tone of a single act of perception with a minimum of cognitive emphasis; for instance, an unformulated feeling of fear.

CHAPTER IV

ANIMAL BEHAVIOUR IN TERMS OF PERCEPTION

1. *Psychological and physiological explanations of behaviour*

THIS CHAPTER will deal with certain aspects of the behaviour of animals without emphasis on their constitution by sub-agents. It is necessary for the development of the argument to consider and interpret in terms of perception some features of the behaviour of animals of various grades of organization.

Let us begin by recapitulating what we regard, for our present purposes, as the essentials in the act of perception—essentials which may be accepted by those who would reject much of the foregoing account of the process in terms of transmission and prehension of feelings, and concrescent events with all their implications, which Whitehead has developed. As we have already pointed out, the great value of his system for the biologist is that it makes it possible to give an account of the generation of the Central Agent by the bodily sub-agents in a late stage of embryonic development; this account, moreover, can be applied to its persistence and its continued relation to those sub-agents after it has been generated. In the present chapter, however, we are concerned with features of the process of perceiving which do not involve those special features of Whitehead's system.

In sensory perception meaning is given to *sensa*; it settles the way in which the percipient is to play its part as a causal agent in the nexus of processes which is its external world. Experience of *sensa* is experience of the effect of its external world upon the percipient, and anticipations and purposes mark the transition of the percipient from an effect of its external world to a cause acting upon that world. As we have already discussed, anticipations and purposes can be coupled together, for anticipations, even when they are of something about to happen to the percipient, imply the potentiality of appropriate purposive action. The meaning of the *sensum* is therefore primarily the anticipations which it evokes. In their most general form—that is, with the minimum of cognitive analysis—anticipations can have little content apart from their affective tone. The object or situation is perceived as one to be accepted or avoided, as attractive or fearful, and so on.

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Modes of perceptions may be instinctive or learnt. In the latter case they are instinctive perceptions modified by experience, for the basis of all perceiving must lie in the constitution of the Central Agent as generated in the processes of embryonic development. Judged by behaviour, instinctive and learnt perceptions may be essentially identical, or, at any rate, effectively identical. This is exemplified when an animal is trained to avoid an object or situation which previously it instinctively sought, or vice versa.

We must now turn to certain types of animal behaviour for which causal descriptions have been given in purely physiological terms. We shall attempt to show that these explanations are inadequate if offered, as they often are, not as exhibiting the machinery through which perception becomes effective as behaviour, but as a substitute for psychological explanations, and even as demonstrating that psychological concepts are unnecessary for their explanation. If there are rival causal explanations of a class of natural occurrences, that explanation is the most adequate which can be applied to the greatest range of apparently diverse facts and requires the fewest *ad hoc* supplementary hypotheses in special cases. On these criteria we maintain that the psychological explanation is more adequate than the physiological, remembering that the former includes, in fact assumes, a physiological substratum. It must be assumed that in all behaviour, even in the working out of a mathematical problem, there is a sequence of physiological changes in the brain and body which could be exhibited as—and, in fact, is—the chain of physical causation. The contention is that, as discussed in the preceding chapter, mental processes determine that the chain of physical causation should take this course rather than that.

2. *The tropism theory of behaviour*

That tropisms are real factors in behaviour cannot of course be questioned, and the elucidation of the factors concerned in tropistic response has been the motive for many fruitful experiments. Some biologists, however, have drawn from them far-reaching conclusions as to the nature of the responses of living organisms which are not justified by the observations themselves, and are opposed to those upheld in this book. I recognize that the extreme application of the tropism theory of behaviour which I am about to criticize is one which probably only a few biologists accept. Nevertheless the application has been made and has met with some measure of approval.

The most systematic attempt to describe organic behaviour in general, possibly including human behaviour, on the tropism theory is that of Loeb, and therefore I will take his exposition of the theory as an example of an extreme application of it.

If a plant seedling is placed in a horizontal position under conditions in which continued growth is possible, the young root curves downwards and the shoot curves upwards. This is an example of a tropism. The root is positively, the shoot negatively, geotropic. Many insects and other animals, if illuminated by a beam of light, orientate themselves so that they move either towards the source of light or away from it. This is also a tropism, in this case phototropism, which, as in all tropisms, can be positive or negative. As, however, there are great physiological differences between the response involved in a plant tropism, in which the directed movement is due to differential growth, and the response involved in an animal tropism which is brought about by its motor organs, the latter are often distinguished as *taxis*; for example, an animal may be positively or negatively phototactic. Following Loeb, however, I will speak of all such responses, whether of plants or animals, as tropisms.

A tropism, then, is a response to some general feature of the environment, such as gravity, light, heat, contact with solids, and so forth. Moreover, a tropistic response is conceived by Loeb as an automatic one, the causes of which are completely analysable into physico-chemical processes. Loeb builds up his general 'tropism theory of animal conduct' from its simplest manifestation, the response to light by a bilaterally symmetrical animal. He conceives that the orientation and movement to the light of a positively phototropic insect illuminated from one side is brought about in the following way: The greater velocity of photochemical reactions in the eye on the illuminated side causes a greater intensity of nerve impulses to travel down the nerves to the muscles of the opposite side, which therefore assume a greater tension, and contract more forcibly, than the muscles on the illuminated side. Thus when the animal begins to move, it will move in a curve towards the source of light owing to the stronger action of the legs on the shaded side. It will continue to move in a curve till its body is parallel with the beam of light. In this position the two eyes are equally illuminated and therefore the legs on the two sides are equally stimulated and act with equal force. Consequently the animal now moves in a straight line towards the source of light.

Loeb holds that, with the necessary special modifications, this theory can be made to fit the phototropic responses of organisms with asymmetrical light-receptor or motor organs.

We may consider two types of experiments which have appeared to some biologists as conclusive proof of this theory as opposed to theories that the animal is acting purposively, seeking the light and not merely being automatically carried by its muscles in the direction of the light.

Many phototropic insects and other animals, if illuminated under experimental condition by two beams of light converging on the animal at an angle, do not go towards either source of light but to a point between them. If the two lights are of equal intensity, the animal moves along a line which will take it midway between the two lights. If they are of unequal intensities, the direction of motion is along a line which will take it between the two sources of light, but nearer the stronger one. Moreover, the inclination of the line of motion in relation to the two lights is capable of a simple explanation in terms of their relative intensities, and therefore of the photochemical reactions in the two eyes.

Commenting on this, Loeb says that the anthropomorphic explanation of the motion of an animal to the light 'is as erroneous in this as in any other case.' For a man who had lost his way in the dark would go to one of two illuminated houses, and not to a point between them determined by the relative intensities of the two lights. Mast (1938), however, points out that some insects go towards or away from the source of highest illumination, and others tend to go towards definite luminous points. When stimulated by light from two sources, the former usually go to or from a point between the two sources, the latter usually go directly towards one of the two sources. An example of the latter type is the fire-fly. The flashes of light produced by these insects are sex signals. When female fire-flies are emitting their flashes of light, the males fly to one of these points, not, naturally, to a point intermediate between the positions of the flashes. Moreover, since the illumination produced by the female is only a flash, the orientation of the male is carried out in darkness. Thus the male fire-fly, after a momentary illumination, whatever direction he was flying in before, turns in darkness in the direction from which the flash came (Mast, p. 212).

A second experiment sometimes held to prove that a movement in relation to light is purely physico-chemical, is that of covering

or removing one eye of an insect. If this is done, whatever the direction of the source of light, only one eye can be stimulated. The animal acts therefore as if it were continuously illuminated by a beam of light from the side of that eye, and travels round in circles, keeping the functional eye on the inside of the circle if the insect is positively phototropic—that is to say, it continuously turns towards the side which is, to it, the illuminated side. A negatively phototropic insect travels in circles with the functional eye on the outside. When performing this experiment certain other factors have to be taken into account, such as whether the insect was light-adapted or dark-adapted at the beginning of the experiment; nor do all insects behave in this way. Moreover, the insect eye is compound, being composed of a great number of separate elements, and some insects respond differently to rays of light focused by the elements in different parts of the eye (Mast, 1938).

It must be remembered, however, that experiments of this kind, though they reveal a physiological mechanism, furnish no evidence that nothing but a physiological mechanism is concerned. Even if the animal were responding purposively to a perceived situation and trying to approach the light, an insect with only one eye functioning might well perceive the situation as one in which the source of light was on the side of that eye, for, however it was orientated, that eye would be the more intensely illuminated. The fact that it was mistaken as to the nature of the situation may indicate a low level of mental development but has no bearing on the purposiveness or otherwise of its action. The only evidence we can obtain relevant to this problem is by putting some obstacle in its way, or putting out of action the physiological mechanism it is employing, and thus discover whether it will adopt some other means of approaching the light (or the direction from which it must appear to it that the light is coming). If it does not do so, we have still no basis on which to judge whether it is acting purposively or not. It may be that it has no other physiological mechanism available, or it may be that its mental development is not high enough to enable it to use it. If, however, it does adopt some other means of approaching the light, evidence is thereby afforded that it is acting purposively. The following is an experiment furnishing this evidence (Mast, 1938): If the front and hind legs of one side of the insect *Eristalis* are removed, leaving only the middle leg on that side, when the animal is illuminated from one side it uses its remaining front leg to pull itself round to

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face the light. If the two legs have been removed from the right side, and the insect is illuminated from that side, the front leg (of the left side) is extended across the front of the animal towards the light and used to pull the insect round towards the light. If it is illuminated from the left side, the same front leg is extended, but this time to the left, and again used to pull round the animal towards the light. Once orientated, such injured animals proceed slightly sideways, but fairly directly, towards the light with the two eyes continuously unequally illuminated and the action of the legs on the opposite sides not balanced. As Mast says, 'after the operation, the action of the remaining legs changes radically so as to compensate for the loss of the action of those which have been removed. As a result of this compensation the insect proceeds towards the light somewhat sideways in place of directly forward. That is, if *Eristalis* is prevented from going toward the light in the way which usually obtains, it adjusts its responses and goes towards it in another way. This indicates that the attainment of an end in view is involved.'

Further, it may be pointed out that the theory that the observed details of the phototropic response leave no room for purposiveness in the action, even if it were not invalidated by such experiments as this, could still only be applied to responses to different intensities of illumination. It does not seem possible to apply the tropism theory to visual perception of objects. A hunting wasp responds in the same way to the spider whether it sees its prey in dim or in bright light, and whether the image it forms on the retina has the shape of a spider seen from in front, the side, above, or obliquely. In fact, the wasp responds, not to the intensity of the stimulation, nor directly to the stimulus pattern on the retina, but to the meaning which this has for it. In short, the wasp perceives the spider.

The movements of plants in response to the stimulus of gravity or light or certain other factors of the environment are brought about by differential growth leading to curvature upwards or downwards, or towards or away from the light. They are therefore brought about by means which are only in the most general way comparable to the movements of an animal. Nevertheless one cannot but suspect that similar basic causes must be involved in producing such similar effects. Indeed, this similarity of response has been made a reason for the view that psychological

factors are not causally concerned in animal tropisms; for, it is argued, one cannot ascribe to a plant a desire to approach the light.

When comparing the tropistic movements of plants and animals, one has to remember that both these organisms are nexus of living agents, of which the cell is conveniently taken as the unit in both. In plants, however, there appears to be nothing of the nature of a Central Agent. Thus the responses of plants are not responses of an individual as a whole, but of individual cells or nexus of cells, and responses involving large regions of the plant, such as the bending over of a growing shoot to the light, is due to the similar response of a large group of similar cells to the same stimulus. The precise nature of the stimulus does not concern us; the response is acceleration or retardation of growth. Certainly no convincing arguments could be found that this particular form of response, considered in isolation from other cell responses, is a purposive response mediated by the act of perception. It will probably be agreed, however, that the plant cell is comparable to the animal cell in its fundamental features, and therefore that any conclusions we can arrive at in regard to the nature of the responses to stimuli on behalf of animal tissue or embryonic cells can be applied in a general way to plant cells.

3. *Learning*

In tropistic behaviour there is no learning. The anticipations and purposes involved in the perception of the situation which results in the characteristic behaviour are instinctive. We shall now turn to types of behaviour where there is relevant modification by experience, and attempt to show that they involve true learning.

Like instinct, the word 'learning' has also been used in a variety of meanings. One sense in which the word is often used, which we shall exclude as a category of learning, is what has been called 'facilitation.' It is very important to distinguish between true learning by experience and facilitation—a distinction which is by no means always drawn. To quote from a well-known biologist, 'learning however is only one example of a natural process in which repetition of an action facilitates its recurrence. The same condition is exemplified in many non-living systems, as when a stream cuts out a watercourse, or an automobile engine is broken in.' But learning which results in more effective coping

with a recurrent situation is not mere facilitation by repetition. This would result in the facilitation and repetition of less effective as well as more effective ways of dealing with the situation.¹ Effective learning involves experience both of successful and unsuccessful action, and the selection by the animal of action found to be successful. Once the successful action has been found, it may then be 'facilitated' by repetition.

Indeed, a tendency to repetition of former actions irrespective of their experienced consequences, would not only fail to result in learning by experience, but would be fatal, for the mistakes which an animal makes in its attempts to deal with a novel situation must be more numerous than its successes. Moreover, observation confirms common sense by showing that actions which have unpleasant consequences, so far from being facilitated by repetition, become less liable to repetition.

Learning by experience involves the formation of new modes of perceiving. As we have seen, every act of perception involves judgment between possibilities. To perceive an object as *this* implies to perceive that it is not *that*, and this means to attach to the sensum the anticipation of this rather than that future happening. In learnt perceptions this judgment is based on previously experienced consequences of different sensa, or of different actions. We must therefore give a little further consideration to the fact that in ordinary sense perception we are not conscious of comparing, rejecting and selecting. When we perceive a cat we are not conscious of arriving at the conclusion that it is a cat by a process of eliminating the possibility that it might be a dog or an elephant, though as we have seen, the fact that we recognize it both as an animal and as a cat shows that we have made a selection among the various animals that we know. Similarly, we are not conscious of judging between possible behaviours towards familiar objects, though the fact that we recognize an orange as an edible object implies that we have judged between its edibility and its inedibility. Nor are we conscious of the anticipations inherent in every act of perception, though as pointed out in chapter 1, the fact that there were such

1. The examples in the quotation above seem to have been selected in a very arbitrary manner. A stream under certain conditions may cut out a watercourse and so facilitate its flow, but under other conditions it may silt up its channel and thus impede its flow. An automobile engine is constructed so that at first the pistons fit too tightly into the cylinders. After the engine has been running for some time the cylinders become worn to a degree which gives the optimum clearance for the pistons, and the engine is now working at its best. This, however, is only the early stages of a process which results later in the cylinders becoming so worn that they are no longer gas-proof, and working of the engine deteriorates.

anticipations is revealed by our surprise if they are not fulfilled. This is of some importance for the interpretation of the anticipations that must be assumed in instinctive perceptions. In ordinary sensory perception there is no conscious passage from sensum to percept. We just perceive cats and oranges.

The fact that we are not conscious of the judging and anticipating, which analysis shows must have occurred in perceiving, can be explained in terms of the discussion on consciousness in the previous chapter. In the perception of familiar objects the process which is the passage from sensum to percept runs so easily, and the intensity of consciousness is therefore so low, that the stages in the process cannot be discriminated by introspection when the act of perceiving becomes an object of consciousness in a later specious present. When perceiving unfamiliar things, however, or familiar things under difficult conditions such as a dim light, we may be conscious, if not of the process of judging itself, at least of an effort to arrive at a judgment. We are conscious of paying attention to the features of the object in order to find out what it really is. Again, in recognizing which of two very unequal squares is the larger, we are not conscious of judging between them. If, however, the squares are of nearly equal size, so that the decision is more difficult, we are conscious of the effort to judge between them. It is, however, significant that more than one act of perception is involved in deciding the true nature of a thing seen in a dim light, or which of two nearly equal squares is the larger. This differentiates reflective judgment from the intuitive or implicit judgment in direct sensory perception. We first perceive the object one way, and then another, and in a subsequent act compare and judge between the different objects as so perceived. Or we first perceive the two squares and then compare what we have seen. In fact, it is not necessary to go on looking at the squares in order to judge which is the larger; it is a help to continue looking at them, but only because memory images are not so clear-cut and constant as directly perceived objects. This subsequent act, in which former perceptions are compared and judged, is in essence also an act of perception, in which memory images play the part which sensa do in sensory perception.

In learning by experience, then, the consequences of earlier experienced sensa become the basis for new anticipations in later perceptions of the same situation, and the process of learning is

the process by which these new anticipations, rather than the old ones, come to be judged to be the appropriate anticipations.

Before turning to the discussion of experiments on learning in animals, it is necessary to note the fact that animals sometimes form habits which are not obviously accounted for by pleasurable or unpleasurable consequences of earlier performances of these actions. This is familiar to us all in the case of domestic animals; it is also well known that rats and other animals trained to run a maze may form habits of taking certain wrong turnings which take a long time to eliminate. Probably, however, such habits are to be explained on the following grounds: (1) The first performance of the series of actions happened to be accompanied by a pleasant experience which the animal wrongly associated with its action; (2) mere familiarity with a recurrent situation and a particular response to it, even if the consequences of this response are affectively neutral, probably has a slightly pleasant affective tone to an animal whose anticipated experience always has a potentiality of turning out to be unpleasant. There is consequently apt to be a slight feeling of fear, uneasiness, or dislike of any novel situation or novel response to a familiar situation, and conversely a feeling of pleasure in a familiar situation or action.

4. *Conditioned reflexes.*

The great prestige of Pavlov's work on the formation of 'conditioned reflexes' in dogs, and his interpretation of this process in purely non-psychological terms, necessitates some discussion of this work. Where no other date is given, references will be to his *Conditioned Reflexes* (1927).

Pavlov started from the fact that food placed in the mouth of a dog is followed by a secretion of saliva. This is an 'unconditioned reflex.' If some stimulus, such as the sound of a whistle, the display of an illuminated circle, or a tactile stimulus applied to the skin, is presented simultaneously with, or shortly before, the presentation of food, after a number of repetitions of the process saliva will be secreted on application of the stimulus without waiting for the presentation of the food. Pavlov calls this secretion a conditioned reflex. Far-reaching theoretical, and in some quarters even philosophical, conclusions have been drawn from the way in which conditioned reflexes are built up and destroyed.

Pavlov presents his work as a contribution to the physiology

of the cerebral cortex comparable to physiological studies on the reflex arc, and concludes that behaviour involving perception, memory, and so forth is made up of reflexes initiated by 'signalling stimuli' (p. 14).

The reflex which Pavlov makes most use of in his researches is the secretion of saliva. This is one component of the 'alimentary reflex' or 'food reflex.' But, 'Besides the secretory, the motor component of the food reflex is also very apparent in experiments of this kind the dog turns in the direction from which it has been customary to present the food and begins to lick its lips vigorously.' (p. 22). Again, 'In the case of the alimentary reflex the dog turned towards the experimenter, dividing its gaze between him and the source of food and smacking its lips.' He also refers to the investigatory reflex, saying of this: 'I call it the "What-is-it?" reflex In man this reflex has been developed with far-reaching results, being represented in its highest form by inquisitiveness—the parent of that scientific method through which we may hope one day to come to a true orientation in knowledge of the world around us.' (p. 12).

In an important respect, therefore, Pavlov's researches have a motive different from those underlying ordinary physiological investigations of reflex action. He is not merely interested in determining the physiological processes intervening in the cortex between the impact of the physical stimulus on the receptor organ and the physical changes in the gland or muscle which constitute the motor response. He is concerned with the processes by which a stimulus which originally does not evoke the reflex becomes a signal which does evoke it. Thus he is concerned with the physiological processes which accompany mental processes. Discussing the failure to produce a conditioned reflex to a stimulus which succeeds instead of preceding the activity (feeding) he says: 'Since conditioned reflexes play the rôle of signals, they must obviously acquire significance only when they precede in time the physiological activity of which they become signals.' (1928, p. 100.) 'Significance' is not a physiological but a psychological concept, and thus the physiological processes to which he applies the names irradiation, concentration, the formation of new nervous connections by mutual induction of points of excitation and inhibition, and so forth, must be the inferred physiological concomitants of the mental process of acquiring significance. Moreover, the passage quoted above implies that Pavlov regards his own spoken

or written accounts of the conclusions which he draws from his experiments as conditioned reflexes to the stimuli provided by his experiments, and yet considers that they supply knowledge of the physiological processes taking place in the dog's cortex. When, therefore, he infers from the dog's response the types of physiological processes in the dog's cortex which intervene between stimulus and response in the formation of a conditioned reflex, he must be drawing inferences as to the processes accompanying the acquisition by the dog of knowledge of the relation between the sound of the whistle and the arrival of food.

Pavlov's method is to account for the dog's behaviour by inferred physiological processes in the cortex which he defines in terms which make them explanatory of the behaviour. Thus when a dog forms a conditioned reflex to the sound of a whistle (in psychological terms, the dog has learnt by experience that the sound of the whistle means that food is coming) this shows that when two points in the cortex are simultaneously in a state of excitation, the paths by which these points are connected in the cortex become thereby specially marked out.

If a conditioned reflex is established to a stimulus by the usual method of following the stimulus by the presentation of food, and then the stimulus is frequently repeated without giving food, the stimulus ceases to act as a stimulus to the secretion of saliva; this is interpreted as demonstrating the occurrence of a cortical process termed 'internal inhibition' (in psychological terms, the dog has learnt that the stimulus no longer means that food is coming). If a conditioned reflex has been formed to stimulus A, and then this is combined with another stimulus, B, the combined stimulus not being followed by the presentation of food, at first the dog responds to the combined stimulus as it formerly did to A alone. After a time, however, it ceases to respond to the combined stimulus, though it still responds to stimulus A when this is given alone. This, according to Pavlov, indicates a cortical process which he calls 'conditioned inhibition,' thus substituting a physiological inference for the psychological inference that the dog at first failed to recognize the significance of stimulus B, and therefore responded to stimulus A whether or not it was given in conjunction with B, but presently learnt by experience that only when it was not combined with B had it its old significance of food coming.

Again, Pavlov found it impossible to establish a conditioned alimentary reflex to a stimulus which followed the presentation of

food instead of preceding it. If a stimulus such as the sound of an electric buzzer is repeatedly applied and always followed by the presentation of food, after a certain number of repetitions the sound of the buzzer becomes itself enough to evoke the secretion of saliva (and also, as we have seen, of the motor response which we must surely interpret as a lively anticipation of food coming). But if the order of the experiment is reversed, and the buzzer is sounded after instead of before the offering of food, however often the sequence may be repeated, the buzzer will never come to evoke the alimentary reflex (p. 27).² The psychological explanation of this seems very satisfying; since in the second experiment feeding always precedes the sound of the buzzer and never follows it, the dog has no grounds for expecting the buzzer to be followed by food. Pavlov, naturally, accepts this, as the above quotation from his work of 1928 shows. His explanation of it in physiological terms is as follows: The mechanism of the formation of a conditioned reflex depends upon the fact that the coincident excitation of two different points in the cortex leads to a connection being formed between these points (pp. 36, 385). Thus in the formation of a conditioned alimentary reflex, the cortical excitation aroused by the sound of the buzzer, which we must assume has not completely died down by the time the food is presented, is conducted to the cortical centre concerned with the alimentary reflex when this is aroused by the presentation of food a few seconds, or even a minute, later. After a number of repetitions, the conduction paths between the two centres become so marked out that the nervous excitation aroused by the sound of the buzzer is conducted automatically to the alimentary reflex centre even when this is not itself in a state of excitation by its proper stimulus, the presence of food in the mouth. Thus the sound of the buzzer will now itself excite this centre, and therefore set off the alimentary reflex. This being the mechanism of the establishment of a conditioned reflex, it is necessary to find an explanation in these terms for the fact that the conduction bond between the two centres is formed when the auditory centre is excited before the alimentary reflex centre, but not when the alimentary centre is excited before the auditory centre. Pavlov offers the following *ad hoc* explanation: The strong excitation produced by the stimulus of food in the mouth, attracts to it the

2. If, however, the stimulus is given *during* the act of feeding an 'insignificant and evanescent' conditioned reflex may develop, the stimulus later becoming inhibitory. (Pavlov, 1928, p. 99). For a discussion of 'backward association' in rats see Washburn, pp. 268, 332.

excitation of the auditory centre if the latter is aroused *before* the stronger excitation of the alimentary centre; but it inhibits the auditory excitation if this occurs *after* the excitation of the alimentary centre.

It is difficult to criticize the large theoretical claims which Pavlov makes for his work, and also its reception by some enthusiasts, without appearing to belittle its great importance as a contribution to the conditions under which dogs learn, and to the inferences which may be drawn as to the distribution of certain physiological processes in the dog's brain. What has to be criticized, however, is the idea expressed by well-known biologists that it has introduced a new method of biological investigation of conscious behaviour possessing greater validity than investigations purporting to be investigations of memory, judgment, perception of relations, and so on. For example, Hogben, who describes Pavlov's experiments in a chapter with the title 'The Mechanisation of Consciousness,' speaks of the 'supreme philosophical importance' of the work (p. 299). He regards its chief importance to lie in the fact that it shows 'how aspects of behaviour which were formerly referred to the introspective concepts of memory, attention and sensation can now be investigated without departing from the language adopted by physiologists when describing the properties of simple reflex action' (p. 43). One may agree with this without drawing the further conclusion that such introspective concepts are unnecessary for an understanding of the dog's behaviour. Both to Pavlov and Hogben, however, the great significance of the possibility of describing conscious behaviour in terms applicable to reflex responses is that a reflex is a necessary or determined response to a stimulus. A reflex response 'is such that for a given agency under the same external conditions we may expect the same result' (Hogben, p. 42).

Pavlov says (p. 378) the cortical activity 'is determined in every minutest detail.' His experiments, however, do not, and could not, make any contribution to the problem of determinism or indeterminism of animal behaviour or of cortical processes. Whether behaviour is determined or not does not depend on inferences as to the neurological processes accompanying it, nor on analogies with reflex action as understood by physiologists. Experimental evidence for determinism of behaviour must be based on the possibility of predicting it, and the experiments of Pavlov naturally leave this question just where it was. No con-

clusions of philosophical importance could be furnished by the degree of predictability possible in such experiments as these, beyond what are already available from our general experience of the tendency of men and animals to behave in roughly similar ways in similar situations. For not only is no two dogs' behaviour exactly the same in Pavlov's experiments, nor the behaviour of the same dog on different occasions the same, but by the rules of the game these unpredictable differences are automatically referred to unknown differences in the external conditions or in the internal physiological states of the dogs.

More important, however, is the fact that the practical predictability of behaviour is irrelevant to the value of psychological factors in its interpretation. Pavlov finds, indeed, that given a knowledge of the previous history of a dog and of its particular idiosyncrasies (which he shows is very important) he can predict within fairly narrow limits what its responses to a given stimulus will be. But similarly, given a knowledge of a man's mathematical training and ability, one can predict within equally or even more narrow limits what his solution of a mathematical problem will be.

In fact, granting that conscious behaviour is completely 'determined,' which in the context evidently means is the inevitable outcome of preceding events, it does not follow that these events are operative solely as physiological (physical) events and not as mental events. Such a conclusion depends, not on inference from observation, but on a theory of causation implicit in a particular theory of the body-mind relation. Nor can the use of introspective concepts be excluded on the grounds that, whatever their causal status, science can make no legitimate use of them. One accepted test of a scientific generalization is that it makes possible the prediction of what will happen under given conditions. Certainly, for the devising of situations in which a man or a dog will behave in a roughly predictable manner, the concepts of memory, anticipation, perception and purpose are more useful than such concepts as the formation of nervous conduction paths or conditioned cortical inhibition. In planning his experiments, Pavlov, as in all scientific experimentation, aims to set up situations which he hopes will yield fruitful results. In devising such situations, he is plainly guided, not by considerations of what may happen in the cortex but by his knowledge of human mental processes. According to him (p. 385), 'the fundamental mechanism of the development of a conditioned reflex depends upon excitation of

some definite point in the cortex coincidentally with a more intense excitation of some other point, probably also of the cortex, which leads to a connection being formed between these two points.' If that were all, however, a conditioned reflex to the sound of a whistle should be produced if the whistle were sounded continuously and food presented at intervals. Actually, under such conditions a conditioned reflex to the sound of the whistle would not be formed. The tacit, and of course correct, assumption underlying the plan of the experiment is that in order that the dog may learn that the sound of the whistle means that food is coming, experience of the sequence, silence—no food, is as necessary as the experience of the sequence, whistle—food. The reason for planning the experiment on this assumption can only be the recognition that we ourselves would have no grounds to base an anticipation of food following the sound of the whistle unless we were able to compare the two experiences of silence followed by no food and sound followed by food.

5. *Habituation*

The change of behaviour sometimes known as 'habituation' also involves this principle of comparison and judgment, though here it is comparison of the actual consequences of the sensum with the instinctively anticipated consequences, rather than comparison of different consequences of different sensa. It is the discovery that sensa which originally (instinctively) evoked anticipation of important consequences are actually irrelevant. This is illustrated by the gradual loss by captured wild animals of their fear of sights and sounds which at first terrified them. It is indeed apparently a universal feature of animal behaviour that they cease to respond to a repeated innocuous stimulus to which they gave an avoidance response at their first few experiences of it, and may give a similar response after a longer interval in which the stimulus is not applied. This has been investigated in Protozoa, sea-anemones, worms, starfish, insects, spiders and vertebrates. Members of all of these groups respond at first by protective or avoidance reactions to mild stimuli such as sounds, vibrations, sudden alterations of light intensity, or touch, but cease to do so after several, or sometimes after only one or two, repetitions of the stimulus at short intervals. This phenomenon is described and discussed by Jennings, by Holmes under the title 'Diminution of reaction to

repeated stimulation,' by Washburn as 'Cessation of reaction to a repeated slight stimulus,' and more fully by Humphrey as 'Habituation.'

This habituation to repeated innocuous stimuli seems indeed to be a general feature of all animals, and is a common experience in ourselves. We soon cease to notice frequently repeated sounds which distracted us at first. On the other hand, response to painful or harmful stimuli commonly becomes more, not less, violent on repetition. Many attempts have been made to explain these phenomena on purely physiological grounds, without bringing in psychological factors at all. Motor fatigue, sensory adaptation, increasing or decreasing excitability, changes of muscle tonus, all interpreted in purely non-psychological terms, have been used as explanations. It seems certain, however, that motor fatigue can only have a very limited application, for habituation to mild stimuli occurs much more quickly than to stronger stimuli which should lead to a more rapid motor fatigue since the response is more violent. The same applies to sensory adaptation, if this is used with the meaning of sensory fatigue—as, for instance, the using up of a necessary chemical substance which takes time to be replenished. Moreover, habituation takes place so quickly to mild stimulation that sense organs so quickly fatiguable would be constantly out of action in normal life. If, on the other hand, sensory adaptation is used in a psychological sense, such as ceasing to pay attention to the stimulus, then of course the question arises, why does the animal quickly cease to pay attention to repeated innocuous stimuli but continue to pay attention to harmful stimuli?

Probably some of the features of habituation can be attributed to fatigue or sensory adaptation in a purely chemical sense, and no doubt physiological changes could be found running parallel to these changes of behaviour, as they could for all types of behaviour, but the important feature of habituation which must enter into any general explanation of it is that it is only after experience of the innocuous character of the stimulus that the animal ceases to respond to it. A painful stimulus, or one which if continued would become harmful, does not become ignored on repetition but evokes more and more violent response. For example, Jennings found that the protozoan, *Stentor*, quickly ceases to respond to a mild innocuous stimulus such as a current of water suddenly impinging upon it, but if it is subjected to a stimulus of a harmful character it not only does not cease to respond to it,

but responds more and more violently with successive applications of the stimulus.

Both land and water snails have been used to study the process of habituation to repeated mild stimuli of various kinds.³ This, however, only takes place to stimuli which one can confidently assume, both from the nature of the stimulus itself and from the reactions of the snail, are not painful. To a strong stimulus producing a violent response the snail responds more and more strongly on repetition of the stimulus. Both these types of behaviour can be illustrated by the following (unpublished) experiments of my own. Garden snails were allowed to crawl about on a large horizontal glass plate covered with damp blotting paper, and stroked at half minute or minute intervals across the neck, behind the horns or antennae, with a thin copper wire arranged so that the pressure of the wire on the snail's skin was approximately constant at each application. The snail responds to the first few touches of the wire by a complete withdrawal of the head into the shell. With further repetitions of the stimulus, however, the response becomes less and less, and after about a dozen repetitions—though more in some snails and fewer in others—the snail responds by a momentary slight retraction of the horns only, an action which does not interfere with its progress. After perhaps thirty repetitions, the only response is a mere twitch of the end of the horns as the snail glides smoothly on its way. The purely physiological explanation of this habituation has already been mentioned. An alternative explanation is that it is an instance of true learning by experience, involving a new mode of perceiving the situation. The element of comparison and judgment implicit, as we have seen, in every act of perception is here the comparison of the instinctively anticipated consequences of the tactile sensum with the actually experienced consequences, whereby the sensum comes to have a new meaning.

The importance of establishing a psychological explanation of habituation is that this seems to be the only change in behaviour appropriate to past experience which has been indubitably demonstrated in the Protozoa (for example, the case of Stentor mentioned above). Some further facts about the process of habituation strengthen the conclusion that learning by experience, in the sense of a relevant change in the meaning of the sensum, is involved.

There is a perfect gradation between instances of habituation

3. See for example Humphrey, pp. 136-138.

which could conceivably be explained in purely physiological terms and instances where one cannot escape attributing it to learning by experience. We all have experience of losing our fear of a strange stimulus or situation by the discovery that it is harmless. There seem to be no grounds for doubting that the loss of fear of their keeper and surroundings by the higher animals in captivity is a consequence of their experience of their harmless character. It is a general experience of experimenters on the lower animals also that they gradually become used to handling and cease the wild struggles they exhibit in the early days of the experiment. I have had much experience of this in a species of fresh-water crayfish. For several days after capture and bringing into the laboratory they are very difficult to handle, raising their claws in a defensive attitude when they see the experimenter approaching, and wheeling round to keep facing his hand, so that great care has to be taken to avoid a painful nip; when seized, they struggle violently to escape. After some days, however, these manifestations of fear completely disappear. The animals cease to threaten the approaching hand with their claws, and remain quite quiet when picked up. Since this process of habituation to handling takes several days, it cannot be ascribed to the purely physiological processes which might suffice to explain some cases of rapid habituation to a stimulus repeated every few seconds or minutes. It must be attributed to the fact that the animals have learnt by experience that the situation is innocuous. The situation which was at first perceived with the affective tone of fear, with the corresponding defence and escape behaviour, comes to be perceived in a different way.

It would be very arbitrary to ascribe habituation which takes place slowly over a number of days to a process quite different from one which occurs rapidly to a stimulus repeated frequently at short intervals. This can be further illustrated by a well-known experiment of the Peckhams. If a tuning-fork is sounded near a spider in its web, it responds violently by dropping from its web and hanging suspended from it by a thread for a time; then it climbs up the thread again, back into its web. Repeated stimulation in this way evokes the same response for about a dozen times, the distance to which the spider drops, and the time which elapses before it climbs back into its web, diminishing with successive repetitions of the stimulus, till eventually it ceases to pay any attention to it. This result of a single series of stimulations

repeated at short intervals might be interpreted as due to motor or sensory fatigue. But one experiment was continued on the same spider over a number of days. On each of the first fifteen days she dropped several times and then would pay no further attention to the stimulus. On the sixteenth day she would not respond at all. The experiment was continued for ten days more. On only two of these days did the spider drop from the web, and then only once on each day, instead of the five to fifteen times a day during the first fifteen days of the experiment. Taking each day's experiment by itself, the diminution of response after several repetitions of the stimulus on each of the first fifteen days might be interpreted as fatigue, with recovery before the beginning of the next day's experiment. This explanation, however, cannot be applied to its ceasing to respond at all after several days of the experiment. This surely indicates that the spider had learnt by experience the innocuous character of the stimulus, and if the factor of learning has to be introduced to account for the results of the extended experiment, there is no reason for excluding it as an explanation of the similar result obtained by a series of repeated stimulations over a shorter period.

Moreover, it is only to harmless stimuli that animals become habituated. To a harmful or painful stimulus they respond, not less, but more, strongly with repetition. This can be illustrated by further experiments of my own on snails. In these experiments the snails were stroked with the same wire as before, but with an alternating electric current running through it, which passed through the snail and by way of the damp blotting paper to the earth wire. To this stimulus the snail responds much more violently, and with repetition of the stimulus the strength of the response increases, whether measured by the degree of retraction of the body into the shell or by the period which elapses before the snail re-emerges and continues its progress. For example, in one snail the lapse of time from the receipt of the stimulus till the snail was again expanded and ready for the next stimulus was, on successive occasions, 40 seconds, 96 seconds, 57 seconds, 3 minutes, $5\frac{1}{2}$ minutes, $4\frac{1}{2}$ minutes, 8 minutes, 5 minutes, 7 minutes, 14 minutes, $23\frac{1}{2}$ minutes. It is significant also that after the snail has had a few, or sometimes even only one, experience of the electric shock, it will respond even to a mild stimulus, such as the touch of the uncharged wire, a touch of a hair on the antenna, or a tap on the glass on which it is crawling, much more strongly

than it did before the experience of the painful stimulus.⁴ These phenomena are paralleled in the behaviour of all kinds of animals which have been investigated in similar ways. The fact that after several experiences of a painful stimulus an animal responds more strongly even to an innocuous stimulus has been ascribed to a general increase of excitability in a purely physiological sense, such as the accumulation or exhaustion of a chemical substance. It is clear, however, that it is equally compatible with an increasing state of fear, with a tendency to attach the anticipation of harmful consequences to any sudden change in the stream of sensa, even when the new sensum is not itself painful (as we react violently to a variety of harmless stimuli when in a state of fear or anxiety).

It may be that a difficulty in the way of interpreting habituation to repeated harmless stimuli as an example of learning may appear in the frequently very quick cessation of the response. Jennings found that Stentor would respond only once to the very mild stimulation of a current of water suddenly impinging upon it. It paid no attention to a repetition of the stimulus half a minute later. With a slightly stronger stimulus, such as the touch of a fine glass thread, it may react the first and second time only, or for half-a-dozen times and then ceases to respond. A similar quick habituation is a common experience in experiments on animals higher in the scale also. It must be remembered, however, that the avoidance or protective response is an interruption to the normal activities of the animal. Hence it is useful to an animal to be able to learn quickly not to be diverted from its normal activities by the multitude of mild stimuli which it is bound to encounter in its daily life, and which only experience will show whether they signify danger or not. Thus it need not surprise us if this negative learning, as it might be called, takes place more quickly than the kind of learning disclosed in the more unnatural situations set up in many laboratory experiments on positive learning. The function of repetition in the learning process is

4. This may be compared with Pavlov's 'generalization of stimuli' (1927, pp. 110-117). He found that if a conditioned salivary reflex to a specific stimulus is established in a dog by the usual method of always following the stimulus by feeding, the dog will at first respond in the same way to almost any definite sensory stimulus experienced by it in the artificially quietened conditions of the experimental laboratory. The dog will, however, quickly come to differentiate between stimuli which are followed by feeding and those which are not. I have attempted without success to get snails to distinguish between harmless and harmful stimuli, by alternating at one minute intervals two different kinds of stimuli, both in themselves painless, but one of them always followed two seconds later by an electric shock. After a few experiences of the shock the snail responds with increasing violence to both stimuli. This suggests that both in the dog and the snail the response to a stimulus which is the precursor of an experience of importance to the animal is changed as the result of experience, but the snail has less power than the dog of discriminating between the special stimuli which are the signals of an important experience and those which are not.

evidently not an essential one, for learning can take place at the first experience, or on the other hand a stimulus carrying important consequences to an animal may be repeated again and again without the animal appropriately altering its response to it. Though not essential, repetition is, however, obviously an important factor in the learning process; it is not an obstacle in the way of learning, but facilitates the discrimination from the chaotic stream of sensa of the particular sensum, or class of sensum, which constantly precedes an important experience. An animal which causally connected every preceding experience with every succeeding experience would learn very little. Every *post hoc* would be *propter hoc*. Although learning may take place at the first experience of the sequence, such immediate associations of cause and effect, as notorious in human beings, are exceedingly likely to prove mistaken.

6. *Trial behaviour*

Habituation, like Pavlov's conditioned reflexes, are instances of learning where little or no bodily activity of the animals is involved in the establishment of the new meaning of the sensum. Another much-studied process of learning depends upon the tendency of animals to vary the details of their actions when these are not giving the satisfaction of attaining their ends, whether this be escape from immediate sensory displeasure or the achievement of some more remote goal, such as obtaining food. Organisms strive to continue experience which is giving satisfaction and to alter experience which is not. This is the basis of the adjustment of behaviour to circumstances by the method of 'trial and error,' which has been studied in innumerable experiments on animals from Protozoa to man. This very useful term unfortunately carries with it implications of the old associationist psychology in its most extreme form; that is to say, completely random movements directed to no goal, with mechanical elimination of unsuccessful and retention of successful ones according to the principles of frequency, recency and effect. In order to avoid this implication I shall speak of this type of behaviour as trial behaviour.

A typical example of trial behaviour is afforded by Thorndike's classical experiments on cats learning to escape from a cage by pulling a ring which releases the catch of the door.⁵ A cat on its

5. This well known experiment has been repeated by Adams, who finds the transition from random striving to the successful form of action much more sudden than Thorndike reported.

first experience of such a cage tries all its instinctive ways of overcoming barriers. It tries to squeeze through the bars, bites and claws at them, and so forth. Eventually it chances to claw at the ring, and finds the door of the cage open. After a few such chance releases, it perceives that pulling on the ring sets it free, and it now performs this action directly on being put into the cage. At the beginning of the experiment, the situation of finding itself captive in the cage evokes the cat's general instinctive action of escape, but the details of the action are varied as each mode of action proves unsuccessful. The variations of the action are random, but the action in general is appropriate to the situation. The animal does not attempt to escape by rolling on its back, or by scratching itself. The randomness of the action applies only to its details, not to the general type of action, which is directed towards the goal—escape.

Here the general means of attaining its goal is given in the cat's instinctive nature. In a more primitive type of trial behaviour there may be a mere feeling of general dissatisfaction with consequent tendency to change the present state in some unspecified way. There may be a feeling of 'anything but this.' There is nothing unfamiliar to ourselves in this tendency. As long as we are comfortable we feel no incentive to alter our condition, but when we feel pain or discomfort, we get restless and try various ways of obtaining relief. It is even possible to find a rough quantitative relation between the frequency of change of action and the degree of pain, discomfort, or, in general, of dissatisfaction, which accompanies it. In one of my own experiments (1927) water-mites (*Eylais*) were placed in a horizontal glass tube 60 cm. long, so arranged that the water in it could be kept at a constant temperature. The diameter of the tube was such that the animal could easily turn in it, but could not make any other appreciable movements except along the tube. In such a tube the animal swims up and down, reversing its direction after a longer or shorter distance. Each of four animals was left in the tube for an hour, and its track up and down the tube recorded. The average length in centimetres between reversals of direction (not counting the compulsory turns at the ends of the tube) was as follows: At a temperature of 6.5°C ., the average length of run between reversals was 75 cm.; at 12.5° , 193 cm.; at 22.5° , 176 cm.; at 32° , 46 cm.; and at 37° , 7 cm. There are independent reasons for placing the normal temperature for these animals within the range

12.5°-22.5°. It will be seen therefore that at normal temperatures the reversals of direction are at much longer intervals than at temperatures above and below normal, and indeed one is led to the generalization that the rate of change of an action which is unsuccessful in relieving dissatisfaction is a function of the degree of dissatisfaction experienced during its performance.

In the last chapter the experience of the Central Agent was analysed into a temporal nexus of actual occasions (percipient events) united into a nexus by the prehensions by each event of its immediate predecessor, which in turn had prehended its predecessor, and so on, so that a continuity of character persists over a stretch of the nexus. In the higher organisms, especially in man, this continuity of character is sufficiently persistent to constitute the personality of the individual. In lower organisms this continuity of character is probably much less pronounced. There is, of course, always that continuity which depends upon the persistent or developing organization of the creature, but within that general continuity there is probably much less definite persistence of the modifications of experience by the moment to moment action upon it of external stimuli. In the limit, one can conceive of an organism which responded according to its specific nature to each stimulus as it appeared, but in which this response effected no enduring relevant change in the agent at all. In such an organism the meaning of every sensum would be given solely in terms of the present constitution of the organism, without any reference to its own previous experiences. In other words, the organism would completely forget every experience the moment it was past. It would be incapable of regulating its behaviour by trial. The success or failure of any act would not itself influence the next act, whether the acts are separated by a time interval (as in exhibitions of learning as usually conceived) or are successive phases of a continuous action such as the sustained efforts of an animal to escape from an unpleasant situation. Placed in a situation which caused it dissatisfaction, it would indeed strive to escape from that situation, and as long as it failed to escape it would go on striving, but there would be nothing to deter the animal from continuing indefinitely its first response to the situation so long as it remained in that situation. Thus the effectiveness of purposive striving in such an organism would be trivial. Indeed, its behaviour could not be discriminated from the reactions of a physical system

to forces acting upon it, and there would be no reason for attributing purposiveness to it.

Washburn discusses the question of continuity of experience in relation to the amoeba. She says (p. 45): 'It is equally possible that in the absence of memory ideas [which Washburn does not allow to the lower animals], not only must the Amoeba lack processes of imagination and reasoning, but there can be nothing like the continuous self-consciousness of a human being, the "sense" of personal identity, which depends upon the power to revive past experiences. It is even possible that the "stream of consciousness" for an Amoeba may not be a continuous stream at all. Since its sensitiveness to changes in environment is less developed than that of a human being, and there are no trains of ideas to fill up possible intervals between the occurrences of outside stimulation, the Amoeba's conscious experience may be rather a series of "flashes" than a steady stream. And for the Amoeba, again, we must remember that even such a series would not exist as such; the perception of a series would involve the revival of its past members. Each moment of consciousness is as if there were no world beyond, before, and after it.' Nevertheless, the behaviour of an amoeba, especially in such actions as the capture of motile prey described below, often involves a succession of co-ordinated actions, each one intelligible only as continuing the progress of a previous action and requiring a relevant succeeding action if the prey is to be captured. It seems that we must therefore assume that the 'flashes' Washburn refers to are of quite considerable duration, comprising in a continuous stream at least a short section of the series of experiences making up the total life history of the amoeba.

We may suppose that learning in the sense of capacity to profit by a former experience on a subsequent occasion increased with the evolution of sense organs such as those of sight and hearing which enabled the animal to perceive things at a distance. As Washburn has pointed out, an animal which is only receptive to contact stimuli must, if its response is to be effective, respond immediately to the stimulus. If it does not, the action will be too late, whether it is to escape from an enemy or seize a prey. An animal which perceives its enemy or its prey at a distance has time, however, to form a plan of action before the situation becomes critical. Hence there is much more scope for utilizing past experience in finding the meaning of a complex of sensa, and for regulating the course of the action appropriately to that experience.

Experiments indicate that water-mites use no other sense than that of touch to discover their prey, which consists of motile animals. If a mite which has not fed for some time is placed in a vessel full of water, it displays an almost ceaseless activity, swimming rapidly about, up and down, and turning sharply hither and thither. A close study of its method of capturing its prey suggests that the object of this activity is to bring about chance collisions with the water-fleas which are its staple article of diet. If a mite is placed in a small vessel with a few water-fleas, it evidently does not search for them by means of any sense organs capable of perceiving them at a distance. In fact, it appears to be quite unaware of them at the distance of only a millimetre. When however in its tireless zig-zag movements a mite collides with a water-flea, it makes a rapid movement to seize its prey, which may or may not be successful. If the mite only brushes against the water-flea, it swings round in that direction and circles round the spot two or three times. In doing this, it may collide with the water-flea again and be successful in seizing it; if not, it resumes its former movements. That this is the way in which a water-mite discovers its prey is supported by the following experiments (Agar, 1925). Water mites were placed singly in small vessels. In one series of vessels one water-flea was placed with the mite, in a second series two water-fleas, and in others four, eight and sixteen. If the mites really discover their prey by chance collisions with them, the time taken to catch a water-flea should be inversely proportional to the number present. This is found to be the case. Excluding the mites which failed to catch a water-flea within an hour (27 out of 100 experiments), the average times taken to catch one were: One water-flea present, 24.4 minutes; two present, 10.9 minutes; four present, 5.6 minutes; eight present, 3.3 minutes; sixteen present, 1.7 minutes. Thus the average time taken to catch a water-flea is inversely proportional to the number present, that is to say, it is directly proportional to the probability of chance collision with them.

These experiments were supplemented by other experiments (1927) on their capacity to learn by experience in the usual sense of that phrase. The principle of all the experiments was to place the mite at the end of the stem of a Y-shaped trough supported just below water level so that the water in the trough was too shallow to allow the animals to swim freely. The motive for action was to escape from this abnormal situation. On reaching the

point of divergence of the arms of the Y, by a motion half swimming, half crawling, the animal had the choice of taking either the left-hand or the right-hand arm. If it took the left-hand arm it escaped through the open end of it into deep water. If it took the right hand arm, it found its escape prevented by a sheet of glass. In some experiments, moreover, the punishment for entering the wrong arm was reinforced by an electric shock, the unpleasantness of which to the animal was evidenced by its violent reaction to it. Altogether twenty-one principal experiments were carried out, each water-mite being given from 100 to 800 trials in the apparatus. In no experiment, however, did the mite give any evidence of learning to choose the right-hand rather than the left-hand passage. Throughout all the experiments, the entry of one or other passage continued to be made at random, or at least not relevantly influenced by previous experiences.

It is true that one must not conclude from laboratory experiments of this kind that the animals are totally unable to learn by experience in the situations with which they are confronted in nature. But such experiments are no doubt good evidence that their powers of learning are small, since crayfish, which are animals of the same general type of organization, learn a similar task after very few experiences. Crayfish, however, are provided with eyes and olfactory organs with which they can and do perceive objects at a distance, and their general mode of life is consequently on a much higher mental level than that of water-mites.

It would be outside the scope of this work to give any general review of the psychological processes underlying animal behaviour, so far as these can be inferred from experiments. It is only necessary to refer briefly to certain other features of these processes.

Behaviour may be overt, sub-overt, or purely ideational. We may consider these types of behaviour in relation to the learning process, and especially to learning by trial.

Trial behaviour is overt when the trial action is actually performed, and the character of subsequent acts depends on the success or failure of such performed actions. An example of this is the behaviour of Thorndike's cats in the early stages of their learning the method of opening the door. This is trial behaviour in its most primitive form.

Sub-overt behaviour occurs either when the motive to action

is not strong, or when there is a conflict of opposing motives; it is frequently observable in animals which are in the process of learning. As an example of this we can take the behaviour of a rat during the process of learning to escape from a tank full of water by one of two exits, as in McDougall's well known experiment designed to test Lamarckian inheritance. I choose this example as I have several years' experience of the behaviour of rats under these circumstances during a repetition of this experiment.

The tank is divided into three parallel passages by two partitions which stop short of the far end of the tank. At that end, therefore, the three passages communicate. From the near end of each of the side passages a wire ladder leads to a platform above the water-level. The rat is placed in the water in the near end of the central passage. In its search for a way to escape from the water it swims down the central passage, turns right or left into one of the side passages and swims back along this to the ladder and climbs out. Behind a sheet of ground glass at the back of each ladder is an electric lamp which shines through the ladder down the whole length of the passage, illuminating also its communication with the central passage, so that the rat at its starting point in the central passage can see which side passage is illuminated. The ladders are connected with an alternating electric current, in such a way that the rat receives a shock on mounting the ladder. By means of a double switch, the lighting and shocking currents can be thrown together into either ladder, so that the bright passage always leads to the electric shock. The rat can therefore escape from the water by either passage, but by the bright passage only at the expense of an electric shock as it climbs the ladder. Each rat is given six trials a day, with the light alternately on the left and right sides.

At first the rat escapes by either passage indifferently, but after several experiences of the shock it comes to avoid the bright passage and always chooses the dim one.

Although the behaviour of the rats varies in the individualistic way familiar to all persons who have studied the detailed behaviour of animals, the typical course of the learning process is as follows. In the earliest stages of training, the rat swims up to the bright exit as steadily, and apparently as unconcernedly, as to the dim one. Very early in their experience of the apparatus, most of our rats develop a very strong, generally indeed exclusive, preference

either for the right or the left passage, irrespective of whether it happens to be the illuminated one on any particular trial or not. After some experiences of the shock, the rat's behaviour alters. When its favourite passage is not illuminated, it approaches it without perceptible change in its previous behaviour. When, however, it is illuminated it displays hesitation. It shows an unwillingness to leave its starting point in the central passage, or it swims half way down the central passage, and turns back, repeating this perhaps several times. Or it may even turn into the illuminated passage and then swim back again into the central passage, before it finally makes up its mind to take the shock and get out of the water. This hesitation (in typical cases) increases with further experience of the shock, till at last the rat breaks through its habit of always taking the same passage, and begins to take the other when its favourite passage is illuminated. After a further period, usually only a day or two, in which rejection of the bright passage in favour of the dim one becomes more and more frequent, the rat comes to avoid the former altogether. Whichever of the two exits is illuminated, it unfailingly chooses the other. The learning process is now complete. The dim and bright passages are now perceived by the rat as having specific meanings which they had not at first.

Only a person who accepts the principle that it is unscientific to interpret animal in terms of human behaviour could be in any doubt as to the interpretation of the behaviour of the rat in the hesitating stage of the learning process. The rat is anticipating or imagining the experience of climbing the illuminated ladder and getting the shock. This is in conflict with its anticipated experience of escaping from the water. For the first few seconds after being placed in the water, when it sees that its favourite passage is illuminated, the affective tone (fear) of the anticipated pain of the shock is the stronger, and it stays motionless in the water. As the desire to leave the tank increases in strength it makes partial movements towards the exit passage—this brings into greater prominence the anticipated experience of the shock and it stops or returns; eventually the cumulative unpleasantness of staying in the water outweighs the fear of the shock, or its unwillingness to take the unfamiliar passage, and it swims down the bright passage and takes the shock, or else ventures into the unfamiliar one. When once it has taken the latter step, the final achievement of learning, which consists in perceiving the situation

as meaning not merely the general action of avoidance, but the specific action of taking the dim rather than the bright passage, is seldom long delayed.

Sub-overt behaviour, represented by the 'hesitating stage' in learning, is ideational behaviour in which conceptual action tends to overflow incompletely into overt action. It is noteworthy that a similar feature of learning is exhibited by an animal with so differently constituted a nervous system as a crustacean. In experiments of my own, the common Australian fresh-water crayfish, *Parachaeraps*, was tested in an apparatus consisting of a narrow rectangular box, one end of which was divided by a partition, extending for about a third the length of the box, into two passages. Through the right-hand passage the animal could escape, the left being closed at its far end by a sheet of clear glass. The box sloped down gently to the level of the water, into which the animal could escape from the open passage. The crayfish is placed at the upper end of the box in a cell in front of and mid-way between the inner openings of the two passages. On being released from the cell, it seeks a way out of the box into the water, and soon learns that it must choose the right-hand passage in order to do this. In another experiment the animal was liberated from a cell which, instead of being situated mid-way between the openings of the two passages, was opposite the opening of the (closed) left-hand passage. On being liberated, it naturally tended at first to go to the opening immediately in front of it, and found more difficulty in selecting the correct right-hand passage than when liberated from a point equidistant from the two openings. Under these circumstances, one animal continued even after fifty trials to take the nearer and incorrect left-hand passage on about 40 per cent. of occasions. But its behaviour when entering the wrong passage was markedly different from when it entered the right one. On the latter occasions it entered this passage unhesitatingly. But when its forward rush from its starting point took it, as it tended to do, to the nearer opening of the left passage, it generally stopped and hesitated before entering it, and when it did enter it often turned, always to the right, and tried to get through the partition separating it from the correct passage on its right.

In another experiment with a similar apparatus in which the right and left passages were alternately open and closed (by a sheet of clear glass) the open passage was indicated by lighting a small electric bulb over it (or in other experiments, over the

closed passage). The crayfishes never learnt to associate the light with the open or closed passage, even after 400-600 trials, although in this experiment the penalty for taking the wrong passage was not only failure to escape into the water, but also the reception of an electric shock.⁶ As the experiment proceeded, however, the animals got much slower, showing, like the rats, a reluctance to leave the starting cell, and frequently hesitating before entering either of the passages. The observer could have no doubt that failure to discriminate between the passage that led to freedom and the one which led to an electric shock had resulted in a conflict between the motives to escape into the water, and to avoid the shock, with imagined, or at least anticipated, experience both of escaping and of receiving the shock. After 440 trials of one animal, and 600 of another, the use of the lights was abandoned; for one animal the right-hand passage was left permanently open and the left-hand one provided with the electric shock, with the reverse setting for the other animal. The expectation formed from previous experiments was fulfilled, and both quickly learnt which was the correct passage. Both were given eighty trials with this setting of the apparatus, and neither made an error in its last twenty trials. The point of chief interest, however, is that directly they discovered how to avoid the shock and escape, both animals became brisk again, and what one can only describe as confident in their demeanour. After the eighty trials with this setting, the old one with the alternating lights which they obviously cannot learn, was reverted to, and they quickly became extremely slow and hesitant again, sometimes not making any attempt to get out from the apparatus for much more than an hour, instead of the minute or less taken to escape when they knew which was the correct passage.

Purely ideational (or 'implicit') trial behaviour is behaviour confined to the Central Agent; conceptual action does not pass over into stimulation of motor neurones. The imagined experience of the situation resulting from the conceptual action becomes part of the objective datum for the next percipient event, just as the realized experience does in overt trial behaviour. This is what occurs in human thinking, when we think out the solution of a

6. The animals showed no preference for the light or dim passage as such, going approximately as often to the one as to the other, though in a vessel of which part is illuminated and part shaded, they take up their position in the shaded part, showing that they have sensory discrimination between the degrees of illumination used in this experiment. In other experiments in which the electric bulbs were on moveable arms, and were moved towards the animal in a 'threatening' way as it entered the wrong passage and received the shock, the animals still failed to associate the light with the shock.

problem which presents elements of novelty, meaning by this a problem where the necessary detailed connection of actions and ideas of action is not already given in the constitution of the mind, whether innately or as the result of past experience. This is most clearly seen when one thinks out a problem requiring imagined manipulation, as when one considers how to construct some mechanical device. But all thinking directed to ends, all thinking that is not mere passive reverie, involves the same principle, even if there is no possible overt action corresponding to it—as when one thinks out a mathematical or logical problem. In such a situation one behaves on the purely ideational level essentially in the same way as the cat in the puzzle box. The cat's actions are all of the type appropriate in a general way to a cat's innate method of breaking through obstacles, but the details of that general type of action which will be successful in this particular situation have to be discovered by trial; when we are thinking out a problem, ideas which are generally appropriate to the type of problem in question arise to prominence owing to their relevance (the principle of psychological association), and are accepted or rejected according to whether, on trial, they are found to lead towards the required solution or not. Thinking out a problem is trial behaviour on the ideational level, but there is no fundamental difference between this and overt trial behaviour, for all behaviour is an effort to influence future experience relevantly to present experience, and therefore also to the past experience of which the present experience is a continuation.

7. The behaviour of the amoeba

We will conclude this chapter with an account of the behaviour of the amoeba, an example of an animal on much the same level of organization as an embryonic or a tissue cell. While it is very much more, even on the material side, than the mere 'speck of jelly' of popular evolutionary expositions, it is one of the simplest of those living organisms capable of movement, capture of food, and in fact of living an active life. Many modern observers of the behaviour of this creature are agreed that the same psychological concepts, whatever they may be, which are employed in the interpretation of the behaviour of the higher animals must be ascribed, in their degrees, to the behaviour of the amoeba also.

As is well known, an amoeba crawls along the surface of the substratum by a very characteristic process involving the formation

of pseudopodia. If an amoeba which is at rest is about to move in a certain direction, there is an eruption of its substance in that direction, which grows out into a finger-like projection from its body. The substance of the main body of the amoeba streams into the pseudopodium, the growing tip of which continually attaches itself to the substratum, while the hinder end of the animal is continually detaching itself. Thus a movement of the amoeba as a whole is brought about; the animal has the appearance of pouring itself along.

The details of this process have been studied by many observers; it is not possible to give here more than the briefest outline of it. The account is taken mainly from the work of Mast (1926, 1931), which of course includes a great deal of the discoveries of earlier observers, and applies chiefly to the fresh-water species, *Amoeba proteus*, a form just visible to the naked eye.

The amoeba is composed of four layers of material. 1. The centre of the animal is occupied by a fluid substance, the plasmasol. This commonly forms the greater part of the substance of the animal. 2. This is surrounded by a more solid layer, the plasmagel. 3. On the outside of this again is a fluid layer (not present in all places), the hyaline layer. 4. The outer surface of the organism is formed by a delicate membrane, the plasmalemma. It is this that adheres to the substratum during its locomotion. Roughly, however, the amoeba can be pictured as a vessel, often very irregular in shape, composed of plasmagel and filled with fluid plasmasol.

The essential physical changes and movements concerned in the formation of a pseudopodium and in the locomotion of the amoeba are as follows. For simplicity's sake we will visualize the amoeba as of rounded form, at rest, and about to form a single pseudopodium. At the spot where the pseudopodium will appear the inner layer of plasmagel, in contact with the plasmasol, liquefies. That is, it turns into plasmasol. The plasmagel at this spot becomes, therefore, thinner, and bulges out owing to the pressure of the fluid plasmasol in its container of contractile plasmagel. This bulge is the growing point of the pseudopodium, which is advanced by the forcing into it of more plasmasol by continued contraction of the plasmagel over other parts of the body.

The tip of the advancing pseudopodium is therefore covered by a very thin layer of plasmagel, which is continually stretched further and further by inflow of plasmasol into the pseudopodium.

It is, however, prevented from rupture, or if ruptured is quickly restored, by accretions to it due to solidification or gelation of the plasmasol in contact with it, whereby this becomes added to the thickness of the plasmagel. This rebuilding up of the plasmagel proceeds continuously, so that at a short distance behind the growing point of the pseudopodium it has been restored to its original thickness.

At the same time, the inner surface of the plasmagel layer at the hind end of the animal is liquefying and becoming plasmasol, thus counterbalancing the reverse process of turning plasmasol by gelation into plasmagel which is taking place in the growing tip of the pseudopodium.

These movements of plasmasol and plasmagel, and the conversion of the one into the other, have been established largely by close observation of the movements of minute particles suspended in these layers.

Thus, considered merely as a pseudopodium-forming machine, an amoeba can be compared to a rubber ball tensely filled with fluid. The solution of the inner layer of the rubber at one spot weakens it there, with the result that the elastic contraction of the rubber over the rest of the ball forces this part out into a bulge. The fluid in the ball is, however, itself capable of solidifying into rubber. As the projection increases and the rubber covering it is stretched thinner and thinner, it is continually being built up again from material deposited on it from the contained fluid, so that the tip of the advancing projection, the pseudopodium, is kept covered by a very thin layer of rubber which a short distance back from the tip has been built up to normal thickness. The rubber over the hinder part of the ball (which is now elongated into a cylinder) is kept at fairly uniform thickness, in spite of its continuous contraction, by compensatory solution from its inner surface. This also provides the material for the building up of the rubber walls at the growing point of the pseudopodium. In order to account for the continuation of this process it is necessary further to assume that the newly-formed rubber at the growing point comes into a greater state of tension as, by growth of the parts in front of it, it reaches the hinder end of the cylinder. The energy used in the work done by the amoeba in locomotion must be derived from its metabolic processes working through the contraction of the plasmagel.

The process just described would, of course, only result in

changes of shape, not in locomotion, if the advancing tip of the pseudopodium were not continually attaching itself to the substratum through the plasmalemma, and the hind end of the amoeba were not also continually freeing itself from the substratum. This is what actually occurs in locomotion. Very often, however, an amoeba puts out free upwardly directed pseudopodia not in contact with any solid object. No locomotion results from these.

Anyone who has watched a living amoeba will know what an inadequate picture of the animal is provided by the analogy of a rubber cylinder full of fluid, advancing by accretions to its front end made by material dissolved from its hind end. A moving amoeba seldom has only one pseudopodium. It may have half a dozen or more, of which one is the principal one in relation to its present direction of motion. The others, thrown out sideways and obliquely, have the aspect of being exploratory. Usually they are withdrawn after a short time and others are put out in their place. But sometimes the amoeba will follow up the direction of one of these exploratory pseudopodia which thus becomes the principal one, the old principal pseudopodium being then withdrawn. Even the advancing tip of the principal pseudopodium is continually branching out into incipient pseudopodia spread fanwise about the line of advance, as if testing the ground before deciding which of these possible directions of development of the principal pseudopodium shall be followed up, and which suppressed. In an active amoeba, continually putting out and withdrawing pseudopodia in many directions, the local processes of solation and gelation, and of contraction of plasmagel, must form a very complex system varying from moment to moment as new pseudopodia are formed and old ones withdrawn.

This machinery of local conversions of plasmasol into plasmagel and vice versa, with local differences in tension of plasmagel, takes the place in the amoeba of the muscular system of the higher animals. There is naturally no trace of a structural nervous system in the amoeba. Nevertheless, stimuli received at one point on the surface may provoke a response at a distant point. Kepner and Taliaferro described an amoeba which had put out two long pseudopodia forming an acute-angled V. A minute organism, of the type that amoebae feed on, swam in between the two pseudopodia and touched the surface of the amoeba at the angle of the V. The amoeba responded by putting out a small pseudopodium from the inner edge of each of the main pseudopodia, well above the

point where the food organism had touched it. These lateral pseudopodia grew in towards each other, met and fused to form a bridge between the main pseudopodia, thus imprisoning the prey in a comparatively large triangular space. This type of response to the stimulus of food particles, involving action of parts of the amoeba's body distant from the point of stimulation but appropriate to the capture of the prey, is common.

Jennings found that if the tip of an advancing amoeba is violently stimulated by a fine glass rod, the forward movement of this part is stopped, and a new principal pseudopodium is formed, usually on some part of the anterior end of the animal. Thus its course is only slightly altered. If the new direction of movement still leaves the front part of the body exposed to the action of the stimulus, then a new pseudopodium is formed, still further altering the course. This may continue till the original direction of locomotion is reversed.

The process of food intake by an amoeba has been intensively studied. The details of the process are varied in a remarkable way in accordance with the requirements of the situation.

A motionless particle is commonly ingested in a very straightforward way. When the amoeba comes in contact with such a particle it may, of course, continue on its way without paying any attention to it. If, however, it is going to devour it, the tip of the pseudopodium which has touched it flows over and round it until the object is completely enclosed in the amoeba.

The process of ingesting a motile living organism, such as a minute ciliate or flagellate, is more elaborate, and is varied to suit the particular circumstances. A common procedure, when the amoeba is on a flat surface such as a glass microscope slide, is that it puts out two pseudopodia, one on each side of its prey. These grow out to encircle the prey in a wide arc without touching it, and fuse together at their tips to form a closed ring, which may be several times the diameter of the enclosed organism. At the same time a thin sheet of the substance of the amoeba flows out from the angle made by the two pseudopodia with the body. The advancing rim of this sheet spreads along the edges of the pseudopodia forming a roof to the ring; thus the prey, which has not yet been touched and disturbed by the amoeba, is now imprisoned in a dome-shaped chamber, the rim of which rests on the substratum. A floor to this chamber is now formed in the same way as the roof, and the living prey is now completely

enclosed, together with a drop of water, in a chamber lying within the substance of the amoeba. This is a food vacuole, in which the still living prey may be seen swimming actively about for many minutes, or even an hour or two. Eventually, however, it is killed and digested by secretions formed in the protoplasm and diffusing into the food vacuole.

This process of capturing living prey is by no means stereotyped, but varied to suit the particular circumstances such as the size of the prey, and the shape of the amoeba at the moment. For instance, if the space encircled by the pseudopodia is very large, it may be roofed in by the outgrowth of several flat pseudopodia which widen out and fuse together to form a continuous roof; or if the prey swims under a projecting flap of the amoeba, the edges of this may be lowered on to the substratum to enclose it without the formation of any pseudopodia.

Thus in its capture and ingestion of food the amoeba is capable of adjusting its behaviour to circumstances. This must involve the control of local conversions of plasmagel into plasmasol and vice versa, and local contractions of plasmagel, of a very complicated kind.

An amoeba does not ingest all particles or living organisms of suitable size with which it may come in contact. Mast and Hahnert found that it will discriminate between two species of living flagellates similar in size, form and activity (*Monas* and *Chilomonas*). In a culture containing about equal numbers of these two forms, ten amoebae made collectively fifty-six contacts with specimens of *Chilomonas* and sixty-six with *Monas*, resulting in the ingestion of twenty-three of the former and of only one of the latter. Other observers have noticed a similar selection between inanimate particles.

After ingestion, discrimination is exercised in regard to the time during which the food particles are retained in the amoeba. Digestible food is usually retained until it is digested, which takes from eight to twenty-four hours in the case of a *Chilomonas*. I have observed wheat starch grains retained from two to seven days, undergoing a slow disintegration during this time. On the other hand the indigestible spore cases of the fungus *Scleroderma*, from which digestible contents had previously been extracted by boiling with caustic potash and sulphuric acid, and which are freely ingested by the amoeba, were usually ejected after about twenty hours, but varying from twelve to forty-eight. Substances which

are presumably injurious, such as carmine or uric acid crystals, may be ejected after six or seven minutes (Schaeffer).

Some evidence that amoeba can learn by trial has been produced (Mast and Pusch 1925, Mast 1932), but at present the interpretation of these experiments must be considered doubtful. If, however, our interpretation of habituation as true learning with modification of perception is correct, then this type of learning is certainly exhibited by the Protozoa.

We may finish this account of the behaviour of amoebae with a quotation from Jennings, one of the foremost authorities on the behaviour of the lower organisms. He sums up the impressions gained from his studies of this animal as follows (p. 336):

'The writer is thoroughly convinced, after long study of the behaviour of this organism, that if Amoeba were a large animal, so as to come within the everyday experience of human beings, its behaviour would at once call forth the attribution to it of states of pleasure and pain, of hunger, desire, and the like, on precisely the same basis as we attribute these things to the dog.'

CHAPTER V

EMBRYONIC DEVELOPMENT

1. *Some general features of morphogenesis*

IF A biologist wished to select one phenomenon as the cardinal problem of his science, he could not do better than take the problem of embryonic development, or morphogenesis in general, including regeneration as well as embryonic development.

There may be said to be three main problems of embryonic development commonly discussed by biologists. The first is the organization of the egg by virtue of which it, and the cells and other embryonic parts to which it gives rise, possess the potentiality of developing into the adult organism. On the physiological level this is the problem of the organization of the material and of the physical and chemical processes transmitted by the parents to the fertilized egg. So far as differences between the development of different organisms is concerned, it is generally considered that the material for primary consideration is the genes, for differences between individuals, varieties and species in regard to the organization of the egg cytoplasm, its physiological gradients, morphogenetic fields and so on, can in nearly all analysed cases be referred to prior action upon it of the genes. A full knowledge of all these materials and their reactions with one another would, however, only yield an understanding of embryonic development comparable with the understanding of human behaviour which would result from a full knowledge of the anatomy and physiology of the brain. An exhaustive description of a man's action on seeing a coin lying on the ground, stooping to pick it up, and placing it in his pocket, may some day be possible in terms of the physical processes beginning in the receptor cells of his retina and ending with the contraction of muscle fibres. This, however, would be a very incomplete explanatory description of the total behaviour. It leaves out of account the most significant features of the action—the man's perception of the coin as a valuable object and his consequent intention of putting it in his pocket. Similarly a description of the physical factors in morphogenesis considered in abstraction from the mental¹ side of the process can never be more

1. Remembering that 'mental' refers to the 'mental pole' of an actual occasion, and does not necessarily imply that a succession of these actual occasions constitute a temporal *nexus* to which the term 'a mind' could be applied.

than a description of the means by which morphogenesis proceeds.

As the use of psychical concepts for the interpretation of the processes of embryonic development introduces a factor not directly amenable to experimental verification, it is interesting to learn Spemann's attitude to the use of such concepts. At the end of his Silliman lectures (1938), in which he sets out the results of the modern period of the experimental study of embryonic development, he says: 'There still remains, however, an explanation which I believe to owe the reader. Again and again terms have been used which point not to physical but to psychical analogies. This was meant to be more than a poetical metaphor. It was meant to express my conviction that the suitable reaction of a germ fragment, endowed with the most diverse potencies, in an embryonic "field," its behaviour in a definite "situation," is not a common chemical reaction, but that these processes of development, like all vital processes, are comparable, in the way they are connected, to nothing we know in such a degree as to those vital processes of which we have the most intimate knowledge, viz., the psychical ones. It was to express my opinion that, even laying aside all philosophical conclusions, merely for the interest of exact research, we ought not to miss the chance given to us by our position between the two worlds. Here and there this intuition is dawning at present. On the way to the new high goal I hope to have made a few steps with these experiments.' While I have no reason to believe that he would agree with the form of the psychical interpretations I have attempted, especially at the end of this chapter, it is reassuring to learn that these are the views formed by the man who is one of the acknowledged leaders in modern developments in this field of experimental research.

I am not suggesting that it will ever be possible to give an account of these mental factors in the way that we can for human behaviour, or, as we can confidently assume, for much of the behaviour of other organisms. Nor do I consider it possible that the egg has any far-reaching preconceived plan of development which it proceeds to put into operation. I conceive of embryonic development as a long train of instinctive actions, but as we discussed in chapter 1, there is no need to suppose that an animal at the beginning of a complex instinctive action envisages the final goal of that action. Each stage of the action may be directed to a hormic goal only a little ahead of the present situation.

As already discussed at some length, the importance of including consideration of the mental factor lies in the conception of the causal connection between stimulus and response being mediated by the act of perception. Stimuli are experienced as *sensa*, and perception consists in giving meaning to the *sensa* in terms of action.

It must be admitted at the outset that any attempt to interpret the process of embryonic development as a long train of instinctive action—or rather, of many trains of instinctive actions by relatively independent agents, the self-differentiating parts—cannot be applied in detail. It is only possible to discuss what is involved in such an interpretation and the general lines on which it must be applied. Any attempt at detailed application would soon land us in unprofitable speculation. We still lack studies of the behaviour under various conditions of embryonic cells, or of the larger agents represented by the self-differentiating parts, comparable to the studies we have for amoebae and some other low forms of animal life. In fact, we need a 'natural history' of embryonic cells and self-differentiating parts, as this term is applied to the animal as a whole, and not merely studies of their anatomy and physiology. We need analyses of their hormic goals analogous to those illustrated by McDougall's studies of wasp behaviour described in chapter 1. Experimental morphogenesis has already made a small beginning of this. We know, for instance, that the potentialities of morphogenetic response possessed by embryonic cells and parts are much greater than is normally exhibited in embryonic development. Examples of this will be given later.

We have also the beginnings of a knowledge of the potentialities of behaviour of isolated embryonic cells which reveal significant parallels to the behaviour of free-living simple organisms. By means of micro-cinematograph photography, Kuhl studied the behaviour of single cells and of cell aggregates isolated out of early newt embryos. Holtfreter has brought together a large mass of observations accumulated by him during many years' work on several species of Amphibia. Holtfreter finds that cells loosely dislocated from late cleavage stages (but not completely separated from each other) soon collect into a smooth ball, the form they would have in the intact embryo. This is achieved by amoeboid movements of the individual cells, involving the formation of short blunt pseudopodia. He shows that this collecting together is not a chemotactic response, but trial behaviour. A detailed study of

the process convinced him that the isolation, or partial isolation, of the cells is itself the stimulus to movement. The cells tend towards a physiological equilibrium which is achieved by a contact as complete as possible with other cells. The movements are essentially random or testing movements, evoked by the lack of contact with other cells, and ceasing when satisfactory contact is established.

Kuhl's observations on wandering early embryonic cells of the newt (*Triturus*) are consistent with this conclusion. The cinematograph records of the movements of these cells in a fluid medium on a microscope slide show that a cell may pass within half its own width of a cell aggregate without being deflected by it, but if it comes right up against an aggregate it may fuse with it. The cinematograph records also yielded the very suggestive result that these embryonic cells move in a more irregular fashion in abnormal than in normal media. Using an arbitrary measure of the number of changes of direction by each moving cell, he found that ten cells in serum from animals of their own species, and therefore in a medium which is chemically nearly normal, made an average of 5.2 changes of direction per unit of time. Cells moving in salt solution through which (a) a continuous, and (b) a high frequency alternating electric current, was passed continuously throughout the experiment, made an average of 14.6 (a) and 10.3 (b) changes of direction in the same time. There is an obvious parallel between this and the behaviour of the water-mite in normal and abnormal temperatures described in chapter IV.

Both Kuhl's and Holtfreter's observations support the view that the movements of these embryonic cells are instances of trial behaviour, elicited by a felt dissatisfaction, and ceasing on the chance achievement of satisfaction. The consequence which this has for the interpretation of the mental factors concerned in such action was discussed in chapter IV.

These observations suggest that if we had studies of the behaviour of embryonic cells as detailed as those we possess for amoebae, we should apply to them the statement by which Jennings sums up his experience with that organism, quoted on page 132.

It must be concluded that the factors which we find in the behaviour of isolated embryonic cells enter also into their behaviour in embryonic development, and that small deviations in the movement of the cells are corrected by trial. Their instinctive actions

are fitted to the details of the situation in the same way as in free-living organisms.

Detailed studies of the movements of differentiated or partially differentiated cells of older embryos, especially of the chick, have been made in great numbers by the method of tissue culture. Small fragments of tissue are cut out from the embryo and placed with aseptic precautions in a drop of blood plasma or other suitable medium. In such circumstances the tissues will live for weeks or months, and even years if the fluid extracted from minced up embryos is used as the culture medium (the best known example of this is Carrel's famous culture of chick embryonic tissue, which has been maintained for more than twenty-five years).

Most if not all types of young embryonic cells show active movement in the abnormal conditions of the culture. The movement is brought about by pseudopodia, by means of which the cells creep over the glass or along any solid support such as may be afforded by the introduction of fine threads of silk or spider's web into the fluid culture medium, or by the coagulation of the medium itself. The cells migrate out of the speck of tissue which was used to start the culture, either independently or in masses. In the latter case they may form a network, or a continuous sheet, of cells, those on the edge advancing by means of pseudopodia, and frequently breaking off and wandering away independently. This has been shown for nearly all types of embryonic cells, including mesenchyme, smooth muscle, heart muscle, the endoderm cells lining the stomach and intestine, and ectoderm.

Movement of cells and cell aggregates brought about by their own activities (and not merely by their being pushed about by differential growth of embryonic parts) plays a large part in normal embryonic development. The passage of the amphibian organizer into the blastocoel and its stretching out to form the strip of chordamesoderm, to be described later, is an active movement of cell masses, not due to differential growth. A particularly striking example of cell migration in embryonic development is the movements of the primitive germ-cells in many insects. In several species these are formed at an extremely early stage of development, sometimes in early cleavage. These cells migrate outside the embryo and lie for a time between it and its investing membrane. Much later in development they migrate back into the interior of the embryo through the pole-cell canal (in species of beetles described by Hegner); this canal is a small opening in

the body wall of the embryo which is the persistent gap left by the original passage of the primitive germ-cells out of the embryo, though differential growth of embryonic parts has altered its position considerably. The germ-cells return into the interior of the embryo through this canal by their own amoeboid activity, and eventually reach their proper places where the ovary or testis will develop.

A second problem of morphogenesis, already touched on in the preceding section, is the problem of regulation. The most spectacular examples of this are afforded by experiments in which the ordinary process of development is artificially diverted, resulting in a course of development which subsequently compensates for the disturbance. Examples of such experiments will be given later. As every descriptive embryologist knows, however, embryos of the same species show minor differences even in normal development which are 'regulated' as development proceeds so that a normally functioning adult is produced.

Not only do variations occur in individual development which are not allowed to interfere with the final result, but during evolution hereditary variations have occurred in the developmental process which do not significantly affect the finished functional structure. Many examples of this could be given. The cases most familiar to the comparative embryologist are afforded by allied species of animals the eggs of which differ in the amount or distribution of yolk. Organs which develop in more lightly yolked eggs from hollow rudiments develop from solid rudiments, in forms in which the embryonic cells contain much yolk. Extreme differences of development depending upon the relative amounts of yolk in the egg can be exemplified from the Crustacea. The prawn *Penaeus*, and the lobster and crayfish, are sufficiently alike in adult structure to be classified in the same order of Crustacea, yet *Penaeus* hatches from its small egg as a minute creature, the Nauplius larva, and passes through a long succession of larval stages before it attains the adult structure; the lobster and crayfish on the other hand have large eggs greatly distended with yolk, and the young which hatch from the eggs have essentially the adult structure. The embryonic stages passed through in these eggs differ very greatly from the free-living larval stages of *Penaeus*, yet adults of closely similar structure result, and such differences as do exist between the adults are not dependent on

the differences of development due to the yolk, for differences of the same type are found between other Crustacea independently of the amount of yolk in their eggs.

Thus in embryonic development various routes may be followed to reach functionally equivalent ends, as in the behaviour of the organism as a whole. Studies of instinctive behaviour show that animals of the same species, or the same animal on different occasions, vary in detail the routes by which they attain their goals. Moreover, hereditary changes in the means by which they attain them have taken place during evolution. No doubt the nest building instinct of birds is inherited from a common ancestor, at any rate within each of the large orders of birds, yet almost every species has its own characteristic way of building a nest.

The third main problem presented by embryonic development is that organs develop 'for' future functioning. In other words, there seems to be no congruity between the processes constituting the development of an organ and the processes which are the functioning of the completed organ. The activities of the cells and parts concerned in the morphogenesis of the eye consist partly in movements giving rise to the shape of the eye and its parts, partly to internal histological changes in the cells by which some of them become the rods and cones of the retina, others conducting neurones, others the transparent cells of the lens, and so on. All of these processes are the necessary precursors of the functioning of the eye as an organ of sight, but none of them have any congruity with the act of seeing itself. This applies to the development of all organs, including, of course, the brain. The movement inwards of certain superficial cells of the chick embryo, followed by certain changes in their internal structure and in their anatomical relations with each other and with the receptor and effector organs, produces a nervous system which functions in such a way that the newly hatched chick pecks at small objects. Parallel processes in the human embryo produce a brain which enables the mind to carry out trains of logical thinking. In such detail are these morphogenetic processes dependent upon the initial constitution of the fertilized egg as to cause the reproduction in the offspring of specific forms of parental ability or insanity in human beings, or of degrees of tameness or wildness in mice.

This incongruity between morphogenetic processes and their results is, however, what we are familiar with in instinctive

behaviour. The completed functional organ is not the hormic goal of the embryonic agents which produced it; it is the biological consequence of this behaviour. The problem of how it comes about that the cell movements and differentiations of the embryo result in organs which serve the function of seeing, digesting and so forth in the completed organism is of the same nature as the problem of how it comes about that the act of mating has the result, certainly not intended by the mating animal, of continuing the existence of the species. Whatever may be the hormic goals of the embryonic agents, they cannot include the utility which the results of their activities will have for the completed organism. The evolutionary process must bear the burden of accounting for the fact that the behaviour of animals and of their embryonic parts have these remote consequences not striven for by the agent itself.

There may be said to be no problem of morphogenesis in the lowest living organisms, at least no problem that one would not be content to solve in purely physical terms. The reproduction of the simplest bacteria is not accompanied by any morphogenesis in the usual sense of the word. The organism divides into two parts, each containing its share of all the constituents of the parent organism, and morphogenesis possibly consists in nothing more than the modelling of the daughter organism into the form of the parent, such as a rod or a sphere. It is possible to conceive of this modelling in terms of surface tension or other molecular and physical forces, comparable to those which cause both parts of a divided drop of oil suspended in water to assume the spherical shape of the parent drop. Even when we come to the more highly organized amoeba, only a minimum of morphogenesis is concerned in its reproduction. Certain changes take place in its nucleus before division, probably essentially of the same nature as those which occur in mitosis in higher organisms, and concerned with ensuring that the two daughter nuclei receive similar shares of the differentiated nuclear constituents. Owing to the almost complete absence of permanently localized structural features in the rest of the organism, the two daughter cells contain their share of all the constituents of the cytoplasm, possibly with the only exception of the contractile vacuole. Since in many species of amoeba there is only one of these, it follows that one of the daughter cells must form a new one. Probably, however, this can form almost

anywhere, dependent upon inessential heterogeneities in the distribution of water in the cytoplasm.

The more elaborate processes of embryonic development in the higher organisms must have evolved with increasing complexity of structure or of life history. Even in most species of the Protozoa the daughter cells produced by fission must undergo a process of morphogenesis to give them the same structure as the parent organism. This is exemplified in its highest degree by the hypotrichous Ciliata. Although these animals consist of a single cell only, they exhibit localized differentiations in the form of permanent organelles of locomotion and feeding. These organisms divide transversely, and consequently the anterior daughter cell lacks the posterior organelles of the parent, and the posterior daughter lacks the anterior organelles. A very elaborate process of morphogenesis takes place in these daughter cells. Without knowledge of what actually occurs one might perhaps have prophesied that it would be found that each daughter cell reproduces the missing parts and so completes itself. This is not the case, however, in the more elaborately organized species of the group. Actually, each daughter cell forms a complete new set of rudimentary organelles, including those which it has taken over from the parent organism. These rudiments are not formed in the positions which they occupy in the functional organism, but arise in a definite area near the nucleus. From their place of origin the rudiments migrate to their proper places in the cell body, and at the same time the organelles taken over from the parent are absorbed. Thus from the parent organism two daughter organisms, each half its size and with properly proportioned parts, are formed. In the early stages of their development these organelles cannot function, because at first they are only rudiments and not yet of the necessary size and form, and also because they are not situated in the right places.

We can, however, better trace the increasing complexity of the developmental process in the higher animals by starting with its origin in connection with increasing complexity of life history rather than of structure. It is here that we find the conditions from which the processes constituting the development of the egg of a higher animal can be derived. Examples are afforded by any protozoan with two or more distinct phases in its life cycle, such as a phase of multiplication by fission alternating with periodical sexual phases. We can take the malaria parasite, *Plasmodium*,

as an example. It is convenient to begin the description of its life cycle with the injection of the parasite into the human blood by an infected mosquito. The Plasmodium individual, at this stage known as a sporozoite, penetrates into a red blood corpuscle, where it assumes an amoeboid form and feeds on the substance of the corpuscle. After it has exhausted this supply of food, it divides several times to form a group of small creatures, the merozoites, essentially like itself except for their smaller size. The rupture of the membrane of the now depleted corpuscle liberates these into the blood plasma, and they attack other red corpuscles, feeding on their substance and again dividing into merozoites. This cycle is repeated again and again, until vast numbers of Plasmodium have been produced and vast numbers of corpuscles have been destroyed. Presently, however, the sexual phase of the life cycle sets in. Certain of the parasites, having absorbed the substance of the corpuscle, do not divide into merozoites but remain intact and quiescent within the capsule of the corpuscle. These are now known as gametocytes.

The assumption of this form by certain of the parasites at this stage is probably a response to a change in their environment caused by the accumulation in the blood of chemical substances which are the products of the parasites themselves, or of antitoxins produced by the infected person.

The gametocytes do not develop any further unless the human blood containing them is sucked into the stomach of a mosquito. If this occurs, the fact is revealed that the gametocytes are of two kinds: male and female. The male gametocyte divides to form four to six male gametes. These are very different in structure from the amoeboid Plasmodium individuals found in the human blood. They are long slender forms, swimming in the fluid of the mosquito's stomach with a rapid undulating movement. At the same time the female gametocytes become transformed into the equivalent of the egg of a higher animal. The male gametes find the female gametes, penetrate and fuse with them to form zygotes. It is unnecessary to give a description of the further stages of the life cycle in which the zygote produces thousands of sporozoites, by which the mosquito transfers the disease to another human being.

The significant feature in this life cycle is that a single cell, the sporozoite, gives rise by repeated cycles of growth and fission to a vast number of descendants. So long as their environment

remains unaltered, these retain their morphological and functional characteristics generation after generation. When, however, the environmental conditions are changed—as on the transfer of the parasites from the human blood to the mosquito's stomach—they respond to this change by becoming organisms, the male and female gametes, which differ greatly in structure and function from the ancestral sporozoite.

This process parallels closely what we find in the embryonic development of the higher organisms. Here the egg divides repeatedly to form a great number of cells. Like the descendants of the sporozoite, these cells are genetically identical, and the differences which arise later in their structure and function arise in response to different environmental stimuli. A difference between the descendants of the sporozoite and those of the egg (the embryonic cells) is that in the former the cells separate and lead independent lives, while in the latter they remain in more or less intimate organic continuity. In the swarm of separate cells descended from the sporozoite, and also in the mass of embryonic cells descended from the egg, differentiation is a response to changed environment. We have already seen the nature of the change of environment in the case of *Plasmodium*. In the developing embryo the changes of environment on which differentiation depends are provided by the functioning of the cells themselves, by which localized morphogenetic fields are produced. These provide the stimuli, often, as we shall see, of a chemical nature, which provoke specific morphogenetic responses on the part of the cells receiving the stimuli. The formation of the medullary plate (the rudiment of the brain and spinal cord) from a tract of cells on the surface of the frog embryo is, as we shall see, a response to a chemical stimulus, and is essentially similar to the response of the *Plasmodium* parasite to the conditions in the mosquito's stomach, which turns it from an amoeboid organism into a gamete.

2. *The development of the eye*

It is necessary to look more closely at the process of embryonic development in the higher animals before attempting a more detailed interpretation of it. As an example of this process we will trace in brief outline the embryonic development of the vertebrate eye. This is a good example to choose, for several reasons. Purely descriptive accounts of the normal development of the eye in a large number of animals have been given in great

detail. Many important factors concerned with its development have been studied experimentally. It is a compact organ, well differentiated both anatomically and functionally from the surrounding tissues. It is a striking example of an organ which cannot begin to function until its long and elaborate course of morphogenesis is completed.

The following short account is based mainly on the process as found in the Amphibia (newts and frogs), as experimental methods of studying the embryonic development of the eye have been more extensively applied in this group than in any other.²

Even before it is laid, the material of the frog's egg has a polar organization, which is expressed visibly both by a graded distribution of the yolk granules embedded in the cytoplasm of the egg, and also by a graded distribution of black pigment on the surface. The pole with the least yolk and most pigment is known as the animal pole, and the opposite one as the vegetative pole. These opposite poles of the egg correspond to the anterior and posterior ends of the future embryo. The gradation of pigment and yolk from one pole of the egg to the other is the visible expression of the first morphogenetic field of the developing egg. It is known as the apico-basal field, or gradient field.

Shortly after the egg is fertilized (which takes place in these animals after the egg has been laid), a second morphogenetic field appears—the dorso-ventral (gradient) field. In some species of Amphibia the presence of this field is also visibly expressed by a 'grey crescent' which makes its appearance in the black superficial pigment of the egg on, or near, the meridian opposite the point where the spermatozoon entered the egg. The apex of the crescent marks the dorsal side of the future embryo. All the main axes of the body are therefore now marked out on the still spherical egg. The antero-posterior axis, the dorso-ventral axis, and consequently the system of right-left or bilateral symmetry are all established, though development as usually understood has not yet begun. The first phase of this development is the division of the egg into two cells, then into four, eight and so on till the original gigantic cell which is the egg has become, by repeated division, a mass of small cells. Soon this mass assumes the shape of a hollow ball

2. A very complete critical review of experimental researches on the morphogenesis of the eye has been given by Mangold (1931). A systematized account of the results of the experimental study of embryonic development and morphogenesis in general is to be found in the text-book of Huxley and de Beer (1934), and in less detailed form in Spemann's book (1938). In this chapter, source references are only given to important researches not, or not fully enough, incorporated in these works.

with an eccentric cavity; this is the blastula stage of development, and the cavity is the blastocoel.

The cells of the blastula are still all alike, except for inessential differences such as the amount of yolk or pigment they contain, which depends on the part of the original egg included in the cell. Experiment shows, moreover, that their developmental capacities are not yet differentiated. Although we can point to certain areas of the blastula, and say that unless the normal course of development is interfered with, this patch of cells will develop into brain, that into gills, and so on, their developmental fate has actually still to be determined and can be altered experimentally. There is one important exception to this statement, however—the region of the grey crescent at the apex of the dorso-ventral gradient field. The differentiation of the parts of the embryo starts from this region and no other. For this reason, this portion of the embryo has been called the 'organizer.'

The grey crescent is at present a part of the wall of the hollow blastula, made visible in many, but not all, Amphibia by its colour. The next phase of development is the phase of gastrulation, in which the region of the grey crescent passes from its superficial position into the interior of the blastula. This is accomplished by a complicated movement. A streaming motion sets in, by which the cells of this region converge towards a narrow area. Instead of piling up at this spot, however, the tissue rolls inwards and works its way into the interior of the hollow blastula and then spreads out again to form a sheet of tissue underlying the upper roof of the blastocoel. This sheet is the chorda-mesoderm, so called because the central strip of it will become the notochord (the precursor of the backbone) and its lateral parts will become mesoderm from which many of the internal organs will develop.

The chorda-mesoderm is, then, the organizer, the material of the grey crescent, which has passed (been invaginated) into the interior of the hollow embryo in the phase of gastrulation. The embryo is now in the gastrula stage.

The chorda-mesoderm is now stretched out as a strip of tissue underlying the upper roof (ectoderm) of the hollow embryo. The ectoderm cells immediately above the strip of chorda-mesoderm then begin to differentiate themselves from the surrounding ectoderm (which will become epidermis), and by a process which need not be described, form themselves into the medullary plate,

which later rolls up and sinks below the surface to form the medullary tube. This is the rudiment of the central nervous system, of which the front part will become brain and the hinder part spinal cord. The rudiment of the brain differentiates into three regions, one behind the other. From the front region there grows out on each side a lateral bulge, the optic vesicle. This is the first visible rudiment of the eye.

Meanwhile the embryo is taking form; in particular, the head is being moulded into shape. When the optic vesicles have grown out far enough to reach the epidermis on the sides of the head, the epidermis in contact with them undergoes a change. The pigment with which the whole epidermis is abundantly supplied begins to disappear from that part of it which is in contact with the optic vesicles. This is the first stage in rendering it transparent, for this patch of epidermis has now become the rudiment of the lens. In its further development it bulges in towards the optic vesicle. The bulge closes into a ball which becomes detached from the epidermis and develops into the lens by a process which it is not necessary to describe.

As the lens rudiment grows in from the epidermis the wall of the optic vesicle with which it is in contact bulges in before it, so that the vesicle, previously in the form, roughly, of a hollow ball becomes turned into the optic cup, assuming a shape which can be compared with a double-walled wineglass, the two walls being continuous round the rim of the glass, and the outer wall passing at its base into the stem of the wineglass, which is the original, persistent connection of the optic vesicle with the brain from which it grew out. This connection is the optic stalk, and the optic nerve will later develop in it. The lens lies in the mouth of the cup.

The process of turning the optic vesicle into the optic cup has the appearance of being the mechanical result of the ingrowth of the lens, as one might press in a soft rubber ball with one's finger until the two walls come into contact. Experiment shows, however, that this is not the case, as a similar transformation of the optic vesicle into optic cup takes place in the absence of any lens to push it in.

Further differentiation of the eye consists principally in (1) the conversion of the cells of the walls of the optic cup into retina. This involves the multiplication of cells and conversion of some of them into the light-sensitive receptors, the rods and cones, and others into the nerve cells with which the rods and cones are

connected and which in turn connect with the brain. Although the original connection of the optic vesicle with the embryonic brain persists throughout this process (as the optic stalk), nervous connection of the retina with the brain is secondary, and is formed by outgrowth of nerve fibres from the nerve cells of the retina through the optic stalk into the brain;

(2) The ingrowth of the rim of the optic cup to form, with addition of other tissues, the iris, and the development therein of the muscle-nerve apparatus for regulating the size of the pupil in accordance with the intensity of the light;

(3) The development of the focussing muscle (in those animals in which this is present) and of the extrinsic muscles by which the eye is rotated in its socket;

(4) The addition of supporting coats (choroid and sclerotic) to the outside of the optic cup;

(5) The conversion of the skin in front of the eye into the transparent cornea;

(6) The formation of the aqueous and vitreous humors, and of many other details of structure.

This is a very general account of the morphogenesis of the eye in the normal course of embryonic development. Experimental methods have thrown important light on some of the factors concerned.

In the blastula stage of development, before the immigration of the organizer into the interior of the egg, any of the superficial cells of the blastula are capable of developing into brain rudiment and hence into optic vesicle and eye. This is shown by the fact that if the organizer region is cut out from one gastrula and grafted into another—say on its side—it will migrate into the interior of its host and stretch out under the epidermal layer of its host to form a strip of chorda-mesoderm, just as if it had been in its proper position. The strip of host tissue overlying this introduced organizer turns itself into medullary plate and tube, although normally it would have formed part of the epidermis of the flank. Spinal cord, brain, eyes and other structures develop from this rudiment in the normal way. In fact, two embryos develop from the one egg. One has developed in its proper place and manner; the other, the secondary embryo, is composite, certain of its organs developing from the graft and others from the host.

The organizer (chorda-mesoderm after invagination) is said to 'induce' the medullary plate out of the overlying indifferent tissue,

and it has been shown that the immediate cause of the induction is the liberation from the organizer of a chemical substance, an 'activator' or 'evocator.' This activates or evocates a morphogenetic field in the responding tissue, whereby it becomes a self-differentiating part. Its further development is autonomous, consisting of changes of form and of intracellular differentiations which are responses of the cells to the field in which they lie.

Thus up to the gastrula stage, before the organizer has got to work, any of the superficial cells of the embryo can become rudiments of the eye, or indeed of many other organs. After gastrulation is complete, and the medullary tube has been formed in response to the action of the organizer, the cells over the rest of the embryo lose their capacity to respond to a second implanted organizer by forming another medullary plate. Their former 'totipotency' has been lost. Certain patches of cells are now committed to form brain and spinal cord, and the remainder of the superficial cells of the embryo have lost the power of doing so.

When the lens develops after the optic vesicles have been formed and grown out from the brain into contact with the overlying epidermis, the story is repeated. Although it has not been proved in this case, there is little room for doubt that the induction of a lens from the epidermis is also due to the liberation by the optic vesicle of a chemical substance which is the stimulus to which the overlying epidermis responds by becoming lens rudiment. Although different species of Amphibia differ in this respect, it has been shown that in some species (1) a lens will not form from the epidermis unless the optic vesicle is there to induce it; (2) any part of the epidermis, say in the flank, will form a lens if an optic vesicle is grafted under it. This lens, formed in a place where it is never formed in nature, and over an optic vesicle severed from its connection with the brain and in foreign surroundings, develops properly and fits into the optic cup. The whole forms a properly differentiated eye, with rods and cones and nerve cells in the retina, and so forth, though, having no connection with the brain, it can of course never function.

As in the case of its capacity to form medullary tube in response to the inducing action of the chorda-mesoderm, so the capacity of the whole epidermis to form a lens in response to an underlying optic vesicle is temporary only. It is lost soon after the normal time for lens formation, so that optic vesicles grafted under the

skin of older embryos can no longer induce a lens from it, though the optic vesicles themselves were taken from embryos of the right age for lens induction.

The temporary nature of the capacity of embryonic ectoderm to be 'determined' in particular directions of development such as brain, retina, or lens, is an example of a general feature of embryonic development. The 'competence' of embryonic cells to respond in a specific way to a morphogenetic stimulus is a passing phase in their life history. Not only is it lost soon after the time in which it is normally brought into play, as we have seen in the case of medullary tube and lens, but it also only arises at more or less definite phases of development. In the experiment of inducing a second embryo from an egg by grafting into it a second organizer, if the egg is too young no medullary rudiment is induced in it till it has reached the proper age. Then the secondary medullary plate appears in the host in response to the grafted organizer simultaneously with the appearance of its proper medullary plate in response to its own organizer. Thus partly as a result of permanent changes in the cells due to their previous responses to other morphogenetic stimuli, and partly possibly by a process of maturation, the embryonic cells in the course of their development lose capacities of response which they once had, and acquire new ones.

The eye is an example of a self-differentiating organ. If an early eye rudiment is cut out and transplanted into another part of the embryo, it goes on with its development, including the differentiation of the rods and cones and nerve cells of the retina. This will take place even in eye rudiments (of chick embryos) removed from the embryo altogether and cultivated in a nutritive medium in a test tube (Strangeways and Fell), though the general shape of the eye becomes very abnormal under these circumstances, probably because of its abnormal environment and lack of surrounding supporting tissues. It is evident, therefore, that the eye rudiment carries a morphogenetic field, and the movements and internal differentiations of its cells depend upon their position in the field, in essential independence of any action upon them from outside.

Dragomirov has shown that in the frog even small fragments of the outer layer of the optic cup transplanted into the tissues of the ear region will bend over, and become thus two-layered

as in the normal optic cup; the outer layer will develop, as in the normal rudiment, into the tapetal layer, and the inner layer, though derived from the part that should have become tapetum, takes the place of the nervous layer of the retina. Such an optic cup will even induce the formation of a lens from overlying epidermis, and development proceeds in essentials normally, though with frequent malformations of general shape due, in all probability, to mechanical influences largely connected with the abnormally small size of the organ; for in this case the eye has to be formed out of only a small fraction of the number of cells normally present.

In the experiment just quoted the optic cup, produced in this strange way and lying in a strange position, induced a lens from the epidermis overlying it. But if an optic vesicle or optic cup is removed to a place where there is no epidermis near it from which it can induce a lens, it will form one for itself out of its own retinal cells. A multiplication of cells takes place in the retinal layer at one point in the rim of the optic cup, forming a protuberance. This becomes larger, gradually filling up the mouth of the optic cup (the future pupil); at the same time the cells lose their pigment and become transparent; they take on the characteristic radial arrangement of the cells of the lens; finally the mass becomes freed from the edge of the retina which produced it, and lies in the pupil as a perfect lens. If the lens is removed from the adult eye by operation, a new lens is formed (in the Urodele Amphibia only) in the same way, from the edge of the iris.

Thus it is plain that the development of the eye, once it is initiated, can proceed without the control of the organism as a whole. What has to be ascribed to the agency of the latter is the production of the correct stimulus at the correct time and place, to which the region of indifferent cells receiving the stimulus responds by becoming eye rudiment; that is to say, by modifying its internal processes in the manner which produces the eye field. But having so responded, the eye rudiment, now become, by virtue of its response, a self-differentiating part, goes on its own way, and its further complicated development can proceed independently of any specific influence of the embryo as a whole. The relation of the developing eye to the rest of the embryo, except for mechanical support, is comparable to that of parasite to host. It draws its nourishment from it, but nothing else

essential to its own development—and if this nourishment is supplied to the eye rudiment in a test tube, its development still proceeds.

The eye therefore develops all the complicated apparatus for forming an optical image on the retina, and for transmitting the resulting nerve impulses to the brain, as an essentially independent entity; its usefulness to the organism as a whole only begins when this development is complete, and moreover depends upon a later formed nervous connection with the brain by means of nerve fibres developing from the retina along the optic stalk. But although the optic stalk—the original connection of the optic vesicle with the brain—is the bridge in which the nerve fibres form, its presence is not, as we have seen, essential to the development of the eye, nor even indeed to the local functioning of its parts. For the retina of transplanted eyes, devoid of all connection with the brain, shows its characteristic response to light and darkness, the cones shortening and the pigment spreading inwards on exposure of the eye to light, and the reverse process taking place in darkness. (Laurens and Williams.)

The secondary nature of the nervous connection between retina and brain is further demonstrated by an experiment of Harrison. He exchanged the eye rudiments between embryos of two species of *Amblystoma* (an animal related to the newt). This involved cutting the optic stalk, and grafting the optic vesicle taken from one embryo into the position of the one removed from the other embryo. Examination of the fully developed eyes two or three months after the operation showed that in many cases the optic stalk of the graft had joined up with the brain of the host and the optic nerve had developed, connecting the retina with the brain (though these belonged, not only to different individuals, but to different species). These eyes moved normally, and gave evidence of function in many cases.

After this brief account of how an egg which has no eyes becomes an animal possessed of eyes, we can return to the interpretation of the process of embryonic development.

3. The interpretation of embryonic development as behaviour

Although we have no knowledge of the steps by which the elaborate processes of embryonic development in the more complex animals have arisen in evolution, we may conceive them as derived from the state of affairs described for *Plasmodium*. The sporozoite

gives rise to its descendants, the separate Plasmodium individuals. The egg also produces descendants, the embryonic cells or cell aggregates. In each case, the descendants of their common ancestor are genetically identical, and all possess at first the same potentialities of specific response to stimuli. The stimuli are provided in the case of Plasmodium by the external medium in which the organisms live; in the case of the cells, or agents of higher grade, of the embryo, which remain in organic connection with each other, the stimuli are provided by their neighbours. In both cases the specificity of response depends upon internal factors, ultimately traceable to the genes. The greater range of morphogenetic responses possible to the cells or other agents of an embryo, as compared with a protozoan individual, is doubtless due to greater differentiation of their gene complexes. Mendelian experiments show that the genes are relatively independent and persistent entities, and that differences of individual genes are correlated with differences of morphogenetic processes. By this we do not mean that differences between the various organs and tissue cells within the same individual depend upon differences in their gene complexes, for normally all the cells of the body have the same genes. But increasing complexity of the gene complex accounts for the increasing range of possible morphogenetic response to stimuli provided by neighbouring parts, including among these responses the processes which in turn provide stimuli for further morphogenetic action.

That the diversity of potential morphogenetic response possessed by the embryonic cells of a higher animal must be correlated with diversity of genes in their nuclei is shown by the effects of gene substitution. The substitution of one allelomorph, or form, of gene A for another results in a change in the colour of the eye; of gene B in a change in the number of joints in the fingers; and of gene C in a chemical difference of the blood affecting its ability to clot. True, we do not know of any gene or group of genes on which depend the more fundamental morphogenetic processes such as the capacity of the embryonic cells of the frog's gastrula to respond to the evocator by becoming medullary plate. A change in a gene which abolished the potentiality to form medullary plate, however, would result in the early death of the embryo, and genetic researches have revealed the fact that by far the commonest form of gene changes or mutations are lethal mutations, resulting in the non-development of the egg, or the death of the embryo at

an earlier or later stage of its development. Thus there is good reason to believe that fundamental as well as trivial processes of morphogenesis depend upon genes for their possibility.

The two main evolutionary changes which made possible the development of the highly organized multicellular organisms from their unicellular ancestors were, therefore, the following:

(1) The tendency of the swarm of cells³ descended from their common ancestor, the egg, to remain together in organic continuity instead of separating as independent individuals. Thus it became possible for the cells or larger aggregates of the developing embryo to provide morphogenetic stimuli for each other, both by emission of evocator substances and through the more intimate relationship existing between the constituent members of a morphogenetic field. Thus also are provided the mechanical supports and barriers which play a part in determining the direction of movement of embryonic parts and the shapes of completed organs. In this mechanical action must also be included the stresses and strains which, as Weiss (1934) has shown, probably play an important part in guiding growing nerves to their destinations.

(2) A great elaboration of the gene complexes upon which depend the inherited potentialities of cells and embryonic parts to provide and respond to morphogenetic stimuli.

Within the present century a great amount of knowledge has been obtained about morphogenetic processes, and about genes⁴ and their mode of action. Here it is only possible to touch in a general way on both these subjects.

The general conclusion to be drawn from genetic researches is that the genes provide the necessary conditions under which the cytoplasm makes specific responses to morphogenetic stimuli. There is no doubt that morphogenetic processes are cytoplasmic processes. The movements of embryonic cells and parts are brought about by the cytoplasm; histological differentiation is

3. I am not forgetting that local differentiations of structure and function are not necessarily dependent upon multiplicity of cells in the organism. This is demonstrated by the more complex Protozoa, while Lillie has shown that a small amount of organ formation can take place in a metazoan egg (*Chaetopterus*) in which cell division has been suppressed by artificial means. Nevertheless, full morphogenesis in the higher organisms is always, in fact, dependent upon a multiplicity of differentiated cells. To avoid any misunderstanding, I may repeat that throughout this book I am speaking of cells as the elementary agents of the organism, partly because they are the smallest units known to be capable of prolonged independent life, and partly to avoid continual repetition of the categories of living agents. Many, if not all, cells are nexus of living agents, represented physiologically by sub-fields in the total cell field; on the other hand, cell aggregates which carry a common field are agents in the sense we have defined, namely, acting causally as units or other agents, including their own sub-agents.

4. Further consideration will be given to the genes in chapter vi.

differentiation of the cytoplasm, or of structures formed in the cytoplasm. The relevant difference between a neurone and a muscle cell is a difference of cytoplasmic organization, not of nuclear, or at any rate of gene, organization.

Theoretically, then, a cell deprived of its nucleus might be capable of life, but incapable of its specific morphogenetic differentiations. Some evidence relevant to this is available. A well-known experiment of Spemann demonstrated that in the newt embryonic cytoplasm without a nucleus cannot carry out the process of division into sub-agents which is the beginning of embryonic development. He ligatured a recently fertilized egg so as to separate it into two portions, one containing the nucleus and the other without it. The two portions remained however connected by a narrow bridge of cytoplasm. The portion containing the nucleus divided into smaller cells in the usual way, while the other remained unchanged. When the nucleated portion had divided into sixteen cells, one of the nuclei slipped through the connecting bridge into the other portion, which then began to develop, cleaving into smaller cells in the usual way. The two portions were now separated completely by rupture of the connecting bridge, and from each portion a perfect embryo was developed. These were reared till they were 140 days old.

Amoeba has been much used for experiments on the behaviour of cell fragments lacking a nucleus, since it is easily cut in half without interference with the normal functions by the operation itself. The portion containing the nucleus shows no significant alteration in behaviour or in its capacity for living and reproducing. The part without the nucleus lives for a considerable time, sometimes (Stolc, 1910) for more than thirty days. Most experimenters, however, have found a week or a fortnight to be about its limit of life. For a few days after the operation the behaviour of the enucleate amoeba does not differ essentially from that of intact organisms. If at first it lacks a contractile vacuole, owing to this having been removed with the portion containing the nucleus, it forms a new one which pulsates normally. Earlier experimenters stated that although enucleate amoebae can produce pseudopodia, locomotion is impossible for them since they are unable to secrete the sticky substance which attaches the advancing pseudopodia to the substratum. Although this is sometimes the case, it is however by no means always so, as later workers have found. Enucleate amoebae often creep about for a week or more

after the operation. They can ingest food particles like normal amoebae, up to at least eleven days after the operation. I have watched enucleate amoebae three to five days after removal of the nucleus capturing living flagellates. In one instance, two flagellates swam up close to the amoeba and attached themselves by their flagella to the glass microscope slide. The amoeba responded to their presence by sending out a broad flap above them; after the flap had got well beyond them, its edges were brought down on to the glass to form a dome enclosing the prey, which had not been touched or disturbed during the process. Next the protoplasm forming the rim of the dome in contact with the glass began to flow inward over the surface of the glass to turn the dome into a closed chamber, which when completed contained one of the flagellates (the other having been somehow left out). The amoeba then crept away carrying the ingested prey in a food vacuole. This method of capturing living mobile prey by first surrounding without touching it is characteristic of normal, intact amoebae (chapter iv).

Earlier workers reported that although enucleate amoebae occasionally ingest food, they cannot digest it. Stolc maintained, however, that in his experiments captured Protozoa were digested up to at least the eleventh day after removal of the nucleus.

Nevertheless, sooner or later enucleate amoebae show obvious signs of unhealthiness. They cease to feed or move, and contract into a ball. From this, short blunt pseudopodia, amounting to little more than temporary irregularities of shape, are slowly protruded and withdrawn for a few days more before the organism dies. The cause of death and of the preceding symptoms is not known. Clark suggests that it is due to cytoplasmic dedifferentiation. We know from experiments in genetics and morphogenesis that the genes are concerned in the production of morphogenetic differentiation. It is also known that some metazoan cells temporarily lose visible structural features during mitosis, when the nucleus is in a state very different from that in the normal functioning cell. Amoeba possesses a definite, though simple and partially reversible, micro-anatomical structure, and underlying this there must be a submicroscopic molecular structure; these must be maintained if its vital processes are to continue. If the nucleus is necessary, not only for the production but also for the maintenance of intracellular differentiation, an explanation is provided for the fact that its removal does not cause immediate death

of the cell, nor even for a time a marked impairment of its activities, but death must eventually ensue as the organization breaks down.

The genes are in the nucleus, and the response, whether it consists of a movement of the cell as a whole or of its internal histological differentiation, is an action on the part of the cytoplasm; therefore the genes are usually conceived as exerting their influence by the emission of chemical substances which diffuse from the nucleus into the cytoplasm. This notion has been specially elaborated by Goldschmidt, who has shown how far the explanation of gene action can be developed in terms of the emission of enzymes (or enzyme precursors) which alter the rates of chemical processes taking place in the cytoplasm. He has also shown what far-reaching effects on the final constitution of organs, or on complex patterns of skin pigments, can be caused by the action of a single gene.

Starting from the assumption that the initial constitution of the gene complex of the egg is such as to result in the provision of these substances at the right times and places, Goldschmidt's work gives a formal description of the factors conditioning successive phases of embryonic development. It is a description, however, purely on the physiological level, comparable to a description of human behaviour in terms of physical and chemical processes taking place in the sense organs, nerves, brain, and muscle. This is not, of course, to be taken as a criticism of Goldschmidt or of the numerous other workers who have interpreted gene action on these lines. They are not attempting to interpret morphogenesis on the level of behaviour, but on the physiological level.

In the higher organisms, then, the gene complex may be conceived as providing the internal environment which determines the physiological state of each cell, and thus supplying the conditions under which it makes specific responses to the morphogenetic stimuli which are provided for it by neighbouring cells or parts, or by the morphogenetic field of which the cell is itself a constituent. This conception is not incompatible with the view that the action of the genes is itself a morphogenetic stimulus, for there is no sharp distinction between the external stimulus and the internal conditions which determine the response to the stimulus. A male animal in which sex hormones are circulating responds to the

visual or olfactory sensum provided by a female in a manner different from the way in which a male lacking the sex hormones responds to such sensa. The visual or olfactory sensum corresponds to the prehended morphogenetic stimulus, and the sex hormones to the influence of the gene complex. But it is also possible to regard the sex hormone as itself a stimulus, prehended as a sensum which has the affective quality of sexual desire, and which even in the absence of stimuli of external origin may lead to the response of searching for a mate. In fact, as described in chapter III, the meaning of a sensum is given by its integration with other sensa, including those of bodily origin, such as those mediated by the sex hormones. Whether the responding agent is the Central Agent of the mature animal, or an embryonic cell, its response is due to its total integrated psychophysical field, and it must lead to arbitrary distinctions if we try to discriminate between modifications of the psychophysical field due to stimuli of external and internal origin. Nevertheless, in morphogenesis there is an important practical distinction between the action of the genes and of morphogenetic stimuli, in spite of their mutual action in determining the nature of the response. The experimental study of morphogenesis has shown that the developmental fate of an embryonic cell depends upon its position relative to the other embryonic parts. Embryonic parts, the developmental fate of which is still undetermined, if removed from their proper places and transplanted into other positions in the embryo, develop into the structures proper to their new positions, and not into the structures into which they would have developed had they been left in their original places. Thus the differences of morphogenetic response resulting in embryonic differentiation depend upon stimuli originating externally to the responding part, though the potentiality of making the response depends upon the internal conditions provided by the gene complex.

An illustration of the relation between genes, and stimuli of external origin, in determining the specificity of morphogenetic response is afforded by the famous experiment of Spemann and Schotté, confirmed and extended by other workers. If a piece of the epidermis from any region of a young frog embryo (gastrula stage) is grafted over the future mouth region of a newt embryo, the frog epidermis differentiates to form the parts of a mouth. That this is a response to a morphogenetic stimulus emanating from the underlying newt tissue is proved by the fact that in its

normal position in the frog embryo from which it was taken this part of the epidermis would not have formed a mouth. But it provides the newt with a mouth characteristic of a frog, not of a newt. In particular, it produces the ventral suckers which are characteristic of frog tadpoles, but not present in newt larvae. Moreover, it produces the horny teeth characteristic of the tadpole, though the newt larva has genuine teeth of the usual vertebrate type. The reciprocal experiment of grafting newt's epidermis in the region of the future mouth of a frog embryo provides the tadpole with a newt's mouth. Evidently then, the gene complexes of the newt and the frog are sufficiently similar to cause the epidermis of both to respond to the mouth-forming stimulus provided by the tissues of either animal, but the differences between their genes result in frog epidermis forming frog mouth and the newt epidermis forming newt mouth. The morphogenetic stimulus provided by the underlying tissues is prehended with the meaning of action of a specific kind resulting in the formation of mouth and its accessory structures, but the cells responding to the stimulus must produce a mouth in their own characteristic way depending upon their gene complexes. This experiment shows that the specificity of response of the embryonic agents is partly dependent upon specificity of stimulus and partly on specificity of the responding agent. The specificity of stimulus is responsible for the grafted epidermis forming mouth tissues, rather than a limb or a lens. But the specificity of the responding agents is responsible for the kind of mouth tissue which will be produced. This, of course, is paralleled in animal behaviour. The response to a stimulus by two animals of different species, or of the same species in different physiological states or with different previous experience, will depend partly on the nature of the stimulus and partly on the specific constitution or present state ('competence') of the animals prehending the stimulus.

Some morphogenetic stimuli have a very low degree of specificity, as exemplified by the neural evocator liberated by the invaginated amphibian organizer. Many different animal tissues can be made to yield a chemical substance which, when introduced into the blastocoele, will evoke a neural tube out of the overlying ectoderm.

An example of high specificity of morphogenetic stimuli is afforded by the formation of plant galls. The significance of these structures for the interpretation of morphogenesis was pointed out by Herbst more than forty years ago.

Plant galls⁵ are formed by a great number of insects, of which the gall-flies of the Hymenoptera are perhaps the most specialized. A few other animals, such as mites, also produce galls, and parasitic fungi cause outgrowths or other modifications of normal growth comparable to galls. We will confine ourselves, however, to insect galls.

Galls are structures produced by the plant in response to the stimulus provided by the insect, and serve as a protection and source of food for the developing larva. The galls induced by different insects exhibit an extraordinary variety of form, specific for each species of insect. They range in complexity from a mere rolling over of the edge of a leaf, to elaborate outgrowths, involving several different plant tissues, which surround the larva. In some cases an opening is left at the apex of the gall, through which the mature insect will eventually emerge. In other cases, the gall forms a closed chamber, which may be subdivided into smaller chambers. The specialization of morphogenetic stimulus provided by the insects is illustrated by the fact that more than 200 different kinds of gall occur on the oak alone. An example of a complex oak gall is the large many-chambered gall of the gall-fly *Andricus californicus*, which may attain twelve inches in circumference. Another example is the familiar smooth spherical woody galls formed on the leaves. The galls formed by another species of oak gall-fly are crowned by an outgrowth of thorns, and in still another the gall consists of a central chamber completely enclosed by a tangled mass of branching thorns. This gall is formed on the twigs, not on the leaves.

It is a very important fact that galls are not merely masses of hypertrophied plant tissue. They are often very complicated structures, involving the conformable development of different tissues, unlike anything which the plant produces by its own unaided ontogenetic processes. This 'organismic' feature of galls applies not only to their structure, but often also to their functioning. Some closed galls split open when the contained insect is mature, thus allowing it to escape. They may even be provided with a lid which opens when the insect is ready to emerge.

The nature of the morphogenetic stimuli which evoke these extraordinary responses by the plant tissues is unknown, but it is probably chemical. All efforts to produce galls by injection into the plant of substances extracted from eggs and larvae of gall-

5. Reviewed by Küster (1911).

producing insects have however failed. Nevertheless, the most reasonable hypothesis is that the stimulus is chemical. In a few cases the stimulating substance may be introduced by the mother insect when she thrusts her egg into the plant tissues, but it is certain that in most cases the stimulus emanates from the egg or larva. However, what we are primarily concerned with is not whether the stimulus is chemical or not, but with the formation of these highly specific structures in response to specific stimuli.

Moreover, the production of galls demonstrates that the potentiality of morphogenetic response possessed by the plant cells and tissues is vastly greater than those normally realized in the development of the plant. A similar reserve of possible morphogenetic responses could be exemplified by many experiments consisting in altering the usual course of embryonic development in animals. Thus we see what far-reaching alterations in adult structure and functioning can be produced by a single gene mutation. This may directly alter the potentiality of structural response by the embryonic cells, or may cause them to produce new morphogenetic stimuli for other parts to which these respond in complicated organized ways which have never before been evoked in the evolutionary history of the organism.

Consideration of the morphogenetic stimuli operating in normal embryonic development leads us back to the morphogenetic fields. Such fields are an example of biological fields, which we encountered in chapter II, and are to be conceived as regions characterised by some organization of physical, chemical or physiological processes, generally exhibiting a decrement of intensity from some point. This point may be more or less centrally situated, as in the fields determining the limb rudiments of the Amphibia, or at one end of the gradient as in the many axial gradient fields studied by Child, or the dorsoventral gradient field of the amphibian egg. A field may extend over a single cell only. The undeveloped egg, as already described, carries a morphogenetic field; the factor responsible for differentiation within a single tissue cell must also be an intracellular field. Very often, however, the field extends over a region comprising a large number of cells. In this case we must conceive of the field as characterised by some spatial continuity of specific activity of the cells made possible by their organic connection with one another. The region carrying a morphogenetic field, whether extending over a single

cell or over many, is an agent in the sense in which we have consistently used this term; it acts causally as a unit. It may do this by concentrating evocators and liberating them as stimuli to other agents. It also provides morphogenetic stimuli to the cells or other sub-agents which are the components of the region carrying the field. The field is a stimulus field to its components; the responses of these are the various cell movements and differentiations varying according to positions of the cell in the field gradient. This leads to the original field becoming sundered into sub-fields.⁶

The region carrying a morphogenetic field is, or may be, a self-differentiating part, not dependent for its further internal differentiation upon specific influences external to itself. As it differentiates into sub-fields, these in turn may become self-differentiating parts. We have seen this illustrated by the differentiation of the optic rudiment out of the brain rudiment, and its subsequent autonomous development. To cite another instance, the limb rudiments of amphibian or chick embryos carry their own morphogenetic fields, for their further development depends merely on suitable food and other general conditions. As Murray has shown, the field carried by the leg rudiment of the chick embryo becomes sundered into smaller fields corresponding to the future thigh, lower leg and foot. These parts, isolated from the limb rudiment before any differentiation has become visible, will develop into their proper parts independently of the rest of the limb, though with some abnormalities of form, probably due to the abnormal mechanical conditions of development of such isolated parts.

Thus it comes about that during a long phase of embryonic development the unitary organism, the egg, is replaced by a multitude of agents, the self-differentiating parts. The further development of these is essentially independent of the fact that they belong to the embryo as a whole. The action of the organism as a whole is only prominent in quite early stages of development, until the determination of the main organs of the body. Immediately after fertilization the main axes of the body are constituted—the apico-basal (future antero-posterior) axis, the dorso-ventral axis, and consequently the bilateral organization. These general topographical fields pervade the development of the embryo in

6. In the case of mosaic eggs, such as those of Ascidiants, the sundering into subfields has proceeded to a considerable degree within the egg itself before it has started to divide into smaller cells.

later stages, as shown by the fact that secondary embryos induced by implantation of an additional organizer generally take up a position parallel to the main embryo (even if the organizer was implanted transversely to the main axis) and eyes, ears and tail develop at the same levels in the two embryos. In fact, the axial gradient fields of Child which we referred to in chapter II are these morphogenetic fields belonging to the organism as a whole and persisting in the adult. But these main fields operate by determining the general character of the parts which will develop at a given level—a head or a tail, an arm or a leg. Once this determination has been given to indifferent embryonic or regenerating material, this becomes a self-differentiating part and can develop henceforward independently of the rest of the organism.

In the attempt, therefore, to interpret embryonic development as instinctive behaviour, we cannot deal solely with the whole embryo as the organism concerned, after the point where it has begun to break up into self-differentiating parts. From this point onwards we must consider these parts as the behaving organisms. Later they become re-united into a unitary organism, especially, though not solely, by the development of the nervous system. Even in the fully functioning adult organism, however, the hierarchies of agents retain their individuality, remaining agents in their own rights as well as forming components of agents of a higher order. Higher order agents are constituted, on the physiological level, by a common specific physiological process distinguishing them from other agents. On the psychological level, as we have seen in earlier chapters, the agents of higher order are nexus of more elementary agents, notably cells, which are perceiving subjects. The organized activity of these agents, upon which the causal unity of the higher order agents depends, may be due to a similarity of sensory and motor dispositions, and therefore of response to similar stimuli; or it may be due to a subject of higher order, a central agent, generated by and including the constituent subjects.

This chapter will be concluded by summarizing some of the parallels that can be drawn between morphogenesis and other types of instinctive behaviour. As we have already dealt with the first two, they can be merely re-stated:

- (1) Embryonic cells, at least in isolation, exhibit trial behaviour. It was maintained in chapter IV that this implies purposiveness.
- (2) Both morphogenetic and instinctive behaviour are directed

to hormic goals, which have biological consequences that were not the end in view of the organism carrying out the action.

(3) Both brain fields and morphogenetic fields are stimulus fields, providing stimuli to which their constituent cells or other agents make specific responses.

The effector action of the brain field is its excitation of efferent neurones, the most conspicuous, though by no means only,⁷ example of these being the motor neurones concerned with muscular action. They are themselves constituents of the field, their vital processes providing its motor dispositions. The excitation of motor neurones by the field can be compared to the stimulation of the constituent cells of a morphogenetic field to make their responses, in the form of movements or internal differentiation. In both cases the action of the fields is to initiate action in their sub-agents, the action then proceeding autonomously in these agents—the motor units on the one hand, self-differentiating embryonic parts on the other hand.

If I decide to put out my arm and grasp an object, very complicated trains of actions are set going in my sub-agents, the nexus of motor units concerned. I have no knowledge of these processes, nor control of them within the motor units themselves. I know nothing of the initiation and transmission of nerve impulses, nor of the processes of contraction of the individual muscle fibres, nor of the complex organization of all these part-actions into the whole, including as it does the conformable contraction of certain groups of muscles and the relaxation of the antagonistic muscles. Once the action has been set in train by excitation of the motor neurones in the brain field it proceeds autonomously, like the development of a self-differentiating part once its internal morphogenetic field has been determined. Moreover, just as in embryonic development the development of the self-differentiating parts can proceed in isolation from the embryo, so all the components of a complex voluntary action can be set in motion individually or in groups by appropriate artificial stimulation even after these parts have been isolated from the organism as a whole.

(4) We have already drawn a further parallel between the brain field and an intra-cellular field; each is considered to be

7. For instance, perception with the affective tone of fear or anger causes increased secretion from the adrenal glands. In the female pigeon, ovulation depends upon the perception of a male, or even sometimes of another female, for visual recognition of the sexes is imperfect in pigeons (Matthews). The secretion by the male pigeon of the 'pigeon's milk' with which the young are fed, and also the extensive preparatory changes in the crop, only take place when the male is able to see the nesting female (Pattel). Innumerable other examples could be given.

the psychophysical field of an agent, the Central Agent of the organism as a whole, and the central agent of the cell considered as an organism. The question therefore arises whether central agents should be postulated for the larger morphogenetic fields, such as the main antero-posterior axial gradient field which persists from the unfertilized egg into the adult, or the fields of the various self-differentiating parts. Are these fields the psycho-physical fields of central agents, or is the unitary action of these fields due solely to a graded community of process in the individual cells which are the carriers of the field?

Being the psychophysical field of an agent means that the total field forms the objective datum for a percipient event which discriminates certain constituent processes of the field in their relation to the whole (the relation of 'meaning') and thereby reorganizes the field so as to provide appropriate stimuli to certain effector constituents of the field. Like the brain field, a morphogenetic field initiates action in its sub-agents which then carry it out autonomously. But the relation between the Central Agent and its sub-agents is a two-way relation. Not only can it excite its effector constituents, but its sub-agents react back upon it, producing changes in the psychophysical field which are experienced as *sensa*, and by virtue of which the Central Agent can not only initiate action, but control it by inhibiting action already in progress and initiating action in other nexus of motor units. The alternatives to be considered are: (1) a morphogenetic field, besides initiating internal regional differentiation into smaller self-differentiating parts, or initiating differentiation in agents external to itself by liberation of evocators or by other means, keeps control over their subsequent development, interfering if things go wrong by providing appropriate new stimuli to correct the errors; (2) the regulation (apart from initiation) of morphogenesis is brought about solely by sub-agents of the order of cells, in that under the conditions provided by the morphogenetic field they only attain satisfaction when they are in certain relations to each other and to external agents. If we accept the first alternative, morphogenesis proceeds analogously to the construction of a house. There is a dominant agent who does not merely give the word *go* to the individual workers, and then leave them to carry out the work by themselves; it continues to direct them, receiving from them and their work visual and auditory *sensa* which have for him the meaning of supplying, in return, a stimulus

to this man to do this rather than that, to another to undo this piece of work or alter that. The rôle of each sub-agent is to respond to specific stimuli provided by the dominant agent, adjusting the details of his response by the process of trial.

If we accept the second alternative, then the process of morphogenesis must be compared with the action of an ant community in building or repairing damage to the nest. The situation, perceived through the sense receptors of a multitude of ants (the cells in morphogenesis), initiates the appropriate activities in them. But there is no dominant agent directing all these individual activities. The repair of the damage is the resultant of the continued action of a number of agents, each responding to the general situation in accordance with its instinctive nature, supplemented by trial adjustments to the details of the situation. If this is the case, the morphogenetic field must be compared with a pure democracy, not an autocracy. There is no co-ordinating central agent. But, as Whitehead suggests, there may be living agents in which the nexus of their processes may at one moment give rise to a unitary process (an actual occasion) which is a feeling subject, and at another revert to a democracy of feeling subjects which constitute a causal unit solely by reason of their mutual action on one another. To understand this idea it must be remembered that, according to Whitehead, the initial phase of any actual occasion, for instance, a percipient event in the Central Agent, is a concrescence or growing together of feelings provided by contiguous actual occasions. He envisages the possibility of a nexus of feelings which may at times undergo concrescence into a subject of a higher order, and at other times remain as the feelings of subjects separate except for their mutual causal action upon each other.

Although it seems impossible to do more than discuss this in an extremely speculative and inconclusive fashion, the matter is so important for a definition of the problem of morphogenetic regulation that some discussion must be attempted.

The most direct reason for attributing a central agent to a region carrying a morphogenetic field, whether the embryo as a whole or a self-differentiating part, would be that it exhibits trial behaviour as a unit. Several authors have suggested that regulation of form-production is effected by the process of trial and error. For instance, Jennings says (pp. 348-9): 'It is perhaps more difficult to apply the method of regulation above set forth

(by trial and error) to processes of growth and regeneration. Yet there is no logical difficulty in the way. The only question would be that of fact—whether the varied growth processes necessary do, primitively, occur under conditions that interfere with physiological processes. When a wound is made or an organ removed, is the growth process which follows always of a certain stereotyped character, or are there variations? It is well known, of course, that the latter is the case . . . It appears not impossible then that regulation may be brought about in growth processes in accordance with the same principles as in behavior. A disturbance of the physiological processes results in varied activities, and among these are varied growth activities. Some of these relieve the disturbance; the variation then ceases and these processes are continued . . . It may be noted that regulation in the manner we have set forth is what in 'behavior' is commonly called intelligence. If the same method of regulation is found in other fields, then there is no reason for refusing to compare the action there to intelligence. Comparison of the regulatory processes that are shown in internal physiological changes, and in regeneration, to intelligence seems to be looked upon sometimes as unscientific and heretical. Yet intelligence is a name applied to processes that actually exist in the regulation of movement, and there is no *a priori* reason why similar processes should not occur in regulation in other fields.'

These views are, of course, in agreement with those maintained in this book. What we are concerned with now is the identification of the agents which carry out this trial behaviour and exhibit this intelligence. To take as an example the extraordinary powers of regulating its form and regenerating lost parts possessed by the amphibian eye; are the agents which exhibit this behaviour the individual cells, or is it the eye as a whole—or at least the embryonic optic vesicle, and the parts of the eye (retina, tapetum, and part of the iris) which it becomes in the adult?

So far as the normal process of lens-formation is concerned, or the other processes by which a lens is produced when normal lens formation is prevented, or the formed lens is removed, there seems little reason to suppose that the optic vesicle does more than provide the stimulus to lens-formation, which then proceeds without further active control by the vesicle. It is true that the lens (in the Amphibia) is not a completely self-differentiating part in the sense that it attains its full development if the optic vesicle (now become optic cup) is removed. If this is done before the lens is

fully differentiated its further development soon ceases and degenerative changes set in. This, however, can be simply interpreted as failure of the lens cells to continue differentiation in the absence of some constant chemical condition supplied by the normal metabolism of the optic cup.

In fact, certain phenomena of lens regeneration make it very difficult to suppose that the optic vesicle—or later the retina—is the agent controlling form-production and internal differentiation of the lens beyond providing the constant conditions under which the lens cells themselves perform this regulation. As we have seen, if a lens is prevented from forming from the epidermis in the usual way, a substitute lens is formed from the rim of the optic cup; or if the lens is removed from the eye of an adult newt, a new lens is formed from the corresponding place, the edge of the iris. This, however, does not exhaust the potentialities of the lens-less eye to provide itself with a lens. If a piece of iris is cut out from the eye of one newt and placed in the posterior chamber of the eye of another newt, so that it lies in the vitreous humor which fills the space between the lens and the retina, this piece of iris will form itself into a lens if the original lens has been previously removed, but not if the original lens has been left in position. In the former case the introduced iris fragment becomes lens under the conditions furnished by the lens-less eye, though there is no cellular continuity between it and the retina (or any other part of the eye). We may accept the suggestion made by Spemann and developed by Wachs, that normal embryonic lens-formation from the epidermis is induced by a chemical substance diffusing from the optic vesicle. Once formed, the lens itself produces a chemical substance which balances or inhibits the action of the substance produced by the optic vesicle, or rather by the retina, as it has now become. If the lens is prevented from forming, or if after formation it is removed, the lens-inducing substance diffusing from the retina is no longer counteracted, and a new lens is produced from the rim of the iris, or even from a piece of iris artificially introduced into the vitreous humor. A diffusion of chemical substances does not, however, seem an intermediary between the iris fragment and the retina, by which the latter could direct and correct the detailed morphogenetic changes required to turn the former into a lens. It seems that we must assume that the necessary specificity of response resides in the iris fragment itself, or in its cells, and that the retinal secretion merely provides the general conditions to

which the iris cells make their specific response without further detailed control by the retina.

Perhaps the chief general difficulty in ascribing a central agent to a larger morphogenetic field such as that of the optic vesicle, by virtue of which it not merely initiates action in sub-agents but controls that action, stepping in and altering it if it is not proceeding to its proper goal, is its ability to form an eye under experimental conditions which can scarcely ever be paralleled in nature. In the case of the Central Agent of the animal as a whole, the nexus of sensory and motor units constituting its sub-agents are, for it, a number of mechanisms by which it attains its ends. Even the most complicated behaviour consists of combinations of actions by these sub-agents. These mechanisms are the products of evolution; organisms with sensory and effector mechanisms which resulted in responses appropriate to the situations in which they found themselves, survived; those whose mechanisms did not have this fortunate result, died. Only those mechanisms could be thus evolved which were effective⁸ in situations occurring frequently enough for ability to deal with them to have significant survival value for the species. Similarly, a cell has at its disposal an evolved motor and sensory disposition providing a great number of possible movements, chemical activities, and (in the case of embryonic cells) of internal histogenetic differentiations. But the means by which experimental derangements of the normal process of morphogenesis are corrected often seem so unlike those that are required under natural conditions that it is difficult to believe that they depend upon adaptively evolved mechanisms.

We have already seen that an isolated fragment of the outer wall of the two-layered embryonic optic cup (which normally develops into the pigment epithelium, the tapetum) will roll over its edges and become two-layered, the inner layer so formed taking the position of the future retina. A similar phenomenon has been described by Wachs in the fully formed newt's eye. It is possible by a simple operation to remove the whole retina and lens, leaving therefore the posterior chamber of the eye lined by the tapetum instead of by the retina. The cells on the torn rim of the pupil (the rim of the tapetum) multiply and grow in towards the centre of the pupil till a complete membrane is formed across the pupillary space. This membrane is concave towards the posterior chamber

8. In combination with trial behaviour, and especially in the higher animals, with learning by experience.

of the eye; by further increase in area it becomes more and more concave, sinking into the posterior chamber and eventually coming into contact with and lining the tapetum, and therefore occupying the position of the old retina. In this new lining to the posterior chamber rods and cones and all the other cell elements of the retina develop; meanwhile a new lens has been forming from the rim of the iris in the way described before, and the complete eye is reconstituted.

Even supposing that the absence of the retina was perceived by the tapetum as meaning the formation of a new one, it is difficult to suppose that it has the particular meaning of proliferating cells from its torn edge to form a membrane across the pupil, and the subsequent processes necessary to turn this membrane into a new retina. It is difficult to believe this, because newts in nature must surely so seldom suffer loss of the retina that provision for its replacement could not have been produced by evolution. Wachs indeed maintains that newt larvae frequently suffer such accidents, chiefly through cannibalistic attacks by their fellows, but certainly it seems to be straining the argument to maintain that this happens frequently enough to have resulted in the evolution of a special provision to compensate for the disaster. Moreover, very seldom can both eyes be injured in this way, and most animals get along well enough with only one eye. On the other hand, the extraordinary nature of this process may have been exaggerated. The only essential difference between this mode of forming a substitute retina and the normal embryonic process seems to be the initial multiplication of cells from the damaged rim of the iris by which a membrane is formed across the pupillary space. Its further increase and bending in till it comes to form a lining to the tapetum are essentially similar to the invagination of the outer wall of the optic vesicle by which the latter becomes optic cup in normal embryonic development. There is indeed much more regulation of the process required than in normal embryonic development, for the details of the process vary considerably according to whether the old retina has been completely removed by the operation, or whether parts of it in the neighbourhood of the iris have been left intact. Whether this regulation is carried out by the individual cells, varying their movements at random until they attain the satisfaction of being in their proper positions, or whether it is carried out by the tapetum, or the developing retina, as a whole, cannot be decided.

The only conclusion we can reach therefore is that, while a Central Agent must be ascribed to the fully developed animal as a whole, and also to cells, the question as to whether a central agent has to be ascribed to agents intermediate in the hierarchy of organization, such as self-differentiating parts, is more difficult to decide.

(5) Embryonic cells have a stock of potential responses, only some of which will be utilized in any one course of embryonic development. This 'stock' of responses is to be considered in the same way as the variety of responses to *sensa*—sights, sounds, smells—in combination with various internal states, potential to an animal, and which gives it its specific forms of instinctive behaviour in specific situations. During embryonic development the range of responses potential to embryonic cells becomes much reduced, and in adult tissue cells one particular form of response becomes specialized and stereotyped. In neurones, for instance, this specialized response is the initiation and transmission of excitations, manifested in embryonic parts in the form of gradient fields. To quote Child (1921, p. 66), who has made a life-long study of this phenomenon: 'Living protoplasm is irritable or excitable, and excitation in a broad sense is conceived to consist in an acceleration of the fundamental activities of protoplasm or, more particularly, those concerned with energy liberation . . . Protoplasm also possesses the capacity to transmit excitation to a greater or less degree or, more strictly speaking, to transmit some sort of dynamic change resulting from excitation at one point, which induces excitation in adjoining regions. These may in turn excite still other regions, and so the process of excitation spreads, irradiates, or is transmitted.'

According to Child, the transmission of nerve impulses is a specialization of this capacity for excitation and transmission of the excitation which is found in embryonic, and indeed in all, cells. In the neurone the potentiality of response has become so restricted that it gives this response to various stimuli, namely all those which can be used experimentally to induce nerve impulses. Although this response is the one by which the neurone fulfils its characteristic function in the body, it has not, however, entirely lost the other forms of response it possessed as an embryonic cell. Like such cells, it has potentialities of response which are not normally utilized. If, for instance, the axon of the neurone is cut, the end grows forward, and when anatomical conditions are favourable, it will

join up again with its end organ. This outgrowth is not a mere passive growth. The end of the axon is not merely pushed forward by the lengthening of the fibre. It advances by pseudopodia thrust out from the advancing tip, and may have to reach its destination by threading its way through obstacles, such as scar tissue developed in its path.

(6) One of the characteristics of morphogenetic fields is that if a portion of the carrier of the field is removed, the remainder will re-organize itself into a similar field of smaller size.⁹ Out of this will differentiate the proper organs, smaller but correctly proportioned to the whole. Examples of this are the re-organization of a portion of a planarian worm into a complete worm of properly proportioned parts, and the development of a fragment of the optic cup into a complete miniature cup. Very many other examples could be quoted, including the familiar one of the development of a whole embryo out of one of the first two blastomeres. The experiments of Lashley described in chapter II show that a portion of the brain field of the rat will also re-organize itself into a similar field of smaller size. His experiments showed that every part of the cortex is involved in the learning process, but learning can take place after removal of any part of it so long as not less than about one fifth of it remains. Moreover, rats which had learnt the maze with an intact brain remembered it after the removal of a large part of the cortex. This indicates a field organization in the cortex accompanying the process of learning, which involves the whole cortex or such parts of it as are present. After removal of a part, the remainder reorganizes itself into a functionally similar field of smaller size. The fact that a certain minimum amount of cortex is necessary for learning the maze, or for retention of what has already been learnt, is paralleled by the fact that structural reorganization of fragments of hydroids or planarian worms does not take place if they are below a minimum size. This cannot be due solely to lack of material, since these fragments have enormously more material than the eggs of these animals, from which complete organisms develop.

(7) Both in embryonic agents and in the completed organism instincts appear and disappear by the process of maturation. The disappearance with age of the sucking instinct of young mammals, and the development of the sexual instinct later, can be compared

9. See Weiss, 1926, 1928, for many generalizations about morphogenetic fields.

with the passing phases of the competence of embryonic agents to respond to specific morphogenetic stimuli.

The interpretation of embryonic development which we have attempted is in terms of the embryonic agents directed to the achievement of their hormic goals. A problem of a different character is presented by the fact that these hormic goals have such extraordinary and remote biological consequences. The acts of embryonic agents by which they attain their goals we conceive to be the acts of purposive agents. But we cannot suppose that their hormic goals include the biological consequences of their activities; that for instance the hormic goals of the agents concerned in the development of the eye include its preparation as an organ of sight. That would be to attribute to them a foresight even greater than we should have to attribute to the mating animal if we held that its intention was not merely to mate, but to ensure the continuance of the species. The fact that the multifarious activities of the numerous embryonic agents, which moreover during a part of the embryonic process develop in essential independence of each other, produce a unitary organism in which the organs function in ways which are by no means a mere continuation of the processes by which they were formed, is a problem of evolution. It is the problem of how it has come about that these agents should have hormic goals with these remarkable biological consequences. As we have already stated, and must now discuss, the only theory which seems at all capable of giving an account of this evolution is the theory of the natural selection of random variations.

CHAPTER VI

EVOLUTION

1. *Natural selection and the survival of the fittest*

IN THIS section we shall not attempt a full discussion of the theory of evolution. Certain propositions in the theory will be taken for granted; among these are the implications of the phrase, 'survival of the fittest,' when taken in its proper context. This qualification is important, for so many of Darwin's critics have seized upon this phrase and used it in an attempt to depreciate the whole theory. What, they ask, is the criterion of fitness? Answer, survival. What determines survival? Answer, fitness. Therefore the phrase is a meaningless tautology. This conclusion can only be arrived at by divorcing the phrase from its context. It is, for instance, by no means always the case that survival or death is determined by fitness or unfitness, or indeed by any other characteristic of the organism in question. If one sparrow perishes on its first weak flight from the nest, and another does not, it does not follow that the second sparrow was more fit than the first—or indeed differed from it in any significant way at all. It may have been that there happened to be a cat in the neighbourhood in one case and not in the other. Indeed, one of the difficulties in assessing the potency of natural selection is the very fact that so much of the death rate does not differentiate between the fit and the unfit. An essential part of the theory is that death or survival does significantly often depend upon features of the organism itself, and not solely on chances of its environment. Another essential part of the context of the phrase 'survival of the fittest' is the proposition that these differences between organisms on which death or survival may depend are often inheritable.

The phrase 'survival of the fittest' is therefore by no means tautological. As used in its proper context it expresses the propositions that individuals exhibit inheritable differences affecting their resistance to factors likely to cause death, and that in a significant proportion of cases these differences do actually determine death or survival. We shall take these propositions as proved, and discuss whether these, in combination with the further proposition that these inheritable differences arise at random, can account for evolution as it has actually occurred.

Before proceeding to this, however, it must be pointed out that this theory of evolution does not require that all the features which differentiate one species from another must have survival value. There is nothing in the theory which excludes the occasional establishment of variations which are neutral for survival, or even slightly harmful if they are correlated with other characteristics of high survival value. It is therefore not valid to argue, as is often done, that the evolution of the human mind must have involved either some internal urge or some external directive force, because it exhibits faculties of no biological utility; for example, high mathematical ability and aesthetic appreciation. Many instances are known in the animal kingdom of organs or parts attaining a size which we are justified in believing not only to have surpassed the limits of biological utility, but to be a positive handicap. Familiar examples are the immense canine teeth of the extinct sabre-toothed tiger, and the antlers of the extinct giant Irish elk. One factor leading to such excessive size of organs has been well investigated—the principle of heterogonic growth studied by Julian Huxley and many others. It would be beyond the scope of this book to discuss this principle and others which have been discovered. The important fact is that the human brain and mind are not unique in exhibiting characteristics which have no biological utility. Of course, the fact remains that the world was so constituted, even before life appeared upon it, that human beings with their mental faculties did in fact evolve, and this is a legitimate basis for very important philosophical and religious conclusions. It is however not legitimate to use the biologically excessive development of the human brain and mind in order to draw conclusions as to the factors which have determined the *course* of evolution, unless these factors are also applicable to the biologically excessive development of the teeth of the sabre-toothed tiger and the antlers of the Irish elk.

2. *The origin of hereditary differences between organisms*

In the preceding chapters we have discussed the nature of the living organism, especially its characteristic of response to stimuli through the intermediation of perception. The conclusion has been reached that this is characteristic not only of the response of the organism as a whole—the Central Agent—in the higher animals, but also of the lowest organisms, and of the living parts of organisms at least as far down in the hierarchy of their

organization as cells, and probably of cell parts. A discussion of biological evolution must start therefore with a primordial organism or organisms which already exhibited this fundamental characteristic, and evolution is the historical process of the development of diverse organisms from the descendants of the primordial organism. The relation between the primordial living organism and inanimate systems was touched upon in chapter III. We will here only concern ourselves with evolution within the world of living organisms.

Basically, biological evolution is the production of a diversity of organisms from a common ancestor. The fact that this process has in the main been characterised by an increasing complexity of organization is its most striking feature, as the word 'evolution' itself expresses. This increasing complexity cannot, however, be considered as an essential feature of evolutionary change. It appears to be a secondary result, a consequence of the fact that complexity often has survival value by enabling the organism to deal more successfully with its environment, or by making possible life in new environments not yet occupied by other organisms. That 'progress,' the evolution of higher out of lower organisms, is not a necessary feature of evolutionary change is shown by the simpler (generally called degenerate) organisms such as parasites which have evolved from more complexly organized ancestors. Nevertheless, the origin of the complex higher organisms from simpler ancestors gives its special form to the problem of biological evolution. Factors which might successfully account for some type of evolutionary change may not be applicable, within legitimate range of probability, to the evolutionary changes which have actually occurred.

Any theory of evolution must be based upon the nature and causes of hereditary differences between parent and offspring, and this means hereditary differences in the process of morphogenesis, whether embryonic or post-embryonic. Morphogenesis is used here, as before, to include the ontogenetic development of psychological and physiological processes, as well as those processes which result in the irreversible structural changes on which depend the embryonic development of the body. To preserve clarity of thought it is very important to fix attention resolutely on the fact that evolutionary change has been a change in the process of morphogenesis, at least in all organisms which reproduce by germ cells or undifferentiated buds or other parts. When we trace the

evolution of the brain, or of the kidney system, by comparing adult structures and arranging them in a hypothetical ancestral series, we are implicitly comparing the results of different morphogenetic processes. Natural selection is generally conceived as acting on adult organisms, and this is no doubt justifiable in the case of those numerous organs which do not function as such in embryonic life; for all those organs, that is to say, which develop 'for' future functioning. No morphogenetic process incompatible with the life of the embryo as a whole could survive, but so long as it is not incompatible with this, the survival value of the morphogenetic process depends upon the functional value of the end result of the process. In the case of organs which function in specific ways during their morphogenesis, their functional value during this period, as well as after their completion, is relevant to the survival or elimination of that morphogenetic process.

As is well known, there are two opposing views as to the origin of the hereditary differences or variations between parent and offspring which are the basis of all evolutionary change. One is that they are completely random, in a sense to be discussed below, and that these random variations have resulted in the evolution of a diversity of organisms from a common ancestor; and moreover, by the process of natural selection, of a diversity of organisms progressively better and better adapted to an increasing diversity of environments. The other view, although of course admitting the overwhelming evidence that such random variation occurs, maintains that there is another and much more important source of variation, which is directed towards the needs of the organism. One variant of this second view adopts the Lamarckian principle; this is based upon the observed fact that organisms show during the course of their lifetime some capacity to improve with practice their powers of dealing with their environment. It is maintained that these improved capacities are in some degree inherited; that is to say, that the process of morphogenesis in the next generation is altered so that the offspring are born with a capacity of dealing with their environment greater than that with which their parents were born. The limitations of Lamarckian inheritance as an explanatory principle of evolution (assuming that such inheritance occurs) will be discussed later. The conclusion will be that its value in this respect is not great.

Other variants of the belief that variation is directed to the needs of the organism involve the notion of some universal

teleological principle, a vital force, or God, or some other factor which produces variations (alters the morphogenetic processes) in prophetic preparation for the uses to which such variations will be put. This type of evolutionary theory will not be discussed here, since such a belief must either be based on considerations outside the province of science, or else be adopted merely because of the believed failure of any scientifically ascertainable process to account for the observed facts. It is the business of a biologist to examine how successfully the process of evolution can be accounted for without recourse to such factors. To ascribe purposiveness to the acts of living organisms, or living parts of organisms, as has been done in the preceding chapters, comes of course into quite a different category from postulating purposiveness in the process of evolution, for in the former case we can identify the purposing agents, examine their behaviour and compare it with that of a similar organism of which we have inside knowledge, namely, man.

The notion of randomness or chance in the appearance of variations has proved a stumbling block to many. By some, these words have even been taken as equivalent to 'uncaused.' No doubt, if that were the case, the words ought to disappear not only from biological, but from everyday, language. It is not necessary, however, to labour the point that these words have not that significance. Another criticism sometimes passed upon the use of these words in evolutionary theory is that they merely imply ignorance of the causes of variation. There is however an important sense in which variations might still be chance or random even if all the causes were known. Chance is a relative term, and as here used means that the variations, having no relation to the needs of the organism, occur by chance in relation to these needs. This conception of chance can be illustrated by the analogy of a card game, where the cards are first dealt out to the players who then use their skill to make the best use of the cards that have fallen to their lot. Up to the point where the cards have been dealt, it is a game of chance. This obviously does not mean that the allocation of the cards to each player has any uncaused element in it. It is the result of the way in which the cards have been played, shuffled and cut in all the previous games in which the pack has been used; anyone with complete knowledge of the previous history of the pack could foretell the composition of each player's hand. But the distribution of the cards at each

deal, though absolutely determined, is not determined in any way in relation to the desires of the players or the rules of the game which is to be played with the cards after they are dealt. Any tendency for variations to appear because they would be useful to the organism would demand some agent who would have the function in the card game of arranging the cards before each deal in the interests of the game or of individual players. Genetic variations are random in that they occur by chance in relation to the needs of the organism, or to the use which the organism will make of them. They are of course caused, but the needs of the organism, or the uses to which they will be put, are not part of the cause. This notion is so familiar to biologists that only experience of the difficulty which persons unfamiliar with biological modes of thought sometimes have of appreciating the meaning of random variation can excuse the introduction of such an elementary matter.

It must be noted, also, that while the word 'random' implies that variation may take place in every *possible* direction, it does not imply that it may take place in every *imaginable* direction. For the genes certainly have a very complex physico-chemical structure, and the ways in which this can change without destroying their essential character must be limited. Moreover, the possible ways in which the course of morphogenesis can be altered must also be limited. Further knowledge on these matters is likely to clear up many of the uncertainties at present confronting the biologist who tries to picture the detailed operation of the factors which have brought about evolution.

Although not dependent upon the modern system of genetics, and historically preceding it, the conception of random variation is now interpreted in terms of mutation¹ of genes, of their segregation and recombination in every act of sexual reproduction, and of their rearrangements within the chromosomes. There can be no question of gene mutations, recombinations, and rearrangements being in any way caused by the needs of the organism or

1. In discussions of evolution by persons not familiar with the modern system of genetics, a mutation is often taken to be a 'sport,' the sudden appearance of a markedly different form of the organism. This idea is largely based on the notion that the so-called mutations studied by de Vries in the evening primrose are typical. It is now known that his mutations were not mutations in the modern sense at all, but partly due to a peculiar form of segregation from the heterozygous *Oenothera lamarckiana*, and partly due to changes in chromosome numbers due to defects in the process of meiosis. In the modern sense, a mutation is the change of a gene into a new form or allelomorph of the gene, or a rearrangement of the genes in the chromosome; the modification of the process of embryonic development, and therefore of adult structure, produced by the new form of the gene complex may be small or great.

by the uses to which the resulting changes in the process of morphogenesis will be put. The genes correspond to the cards in the card game. The organism that has been dealt a good hand, enabling it to play a successful game, survives, and hands on its good cards to its offspring.

As every geneticist knows, the conception that phenotypic² differences which follow Mendel's law in inheritance are referable to differences of genes, which are distributed among the gametes by the mechanism of meiosis, is capable of very wide application even where no Mendelian segregation can be directly demonstrated in inheritance. Examples are afforded by quantitative characters such as size. The facts point to the conclusion that inheritance of such characters is also by means of genes, and that the reason why this is not immediately apparent is that the number of genes, and therefore still more the possible combinations between them, is very large. Moreover, the view that the theory of inheritance by means of genes is of general application receives convincing support from the study of inheritance in asexual reproduction. Here the mechanism which provides for gene recombination is absent, and as expected therefore by the theory, offspring are found to be genetically identical with their parents, except for occasional mutations.

Apart from the dubious factor of Lamarckian inheritance to be discussed later, the discovered facts systematized in the system of modern genetics indicate that the source of the variations which are the raw material for evolutionary change is primarily gene mutation, and secondarily the various combinations and arrangement within the chromosomes of the diversity of genes so produced.

Genes are usually conceived as particles situated in linear order in the chromosomes, a conception which seems abundantly justified by the evidence for their interchangeability between homologous chromosomes, together with recent work on inversions, trans-locations, duplications and deletions of genes or strings of genes within the chromosomes. Goldschmidt, however, has recently (1938) suggested that it is time to abandon the concept of the genes as separate hereditary units. Much depends on the precise meaning of the words 'separate' and 'unit'; no geneticist would suppose that a gene in isolation (if that were conceivable) would

2. The phenotype is the developed organism; the genotype is the initial genetic constitution of the zygote, primarily its gene complex. Identical phenotypes may be of different genotypes, for example, homozygous and heterozygous dominants; and identical genotypes may give rise to different phenotypes if they develop under different environmental conditions. The fertilized egg is a zygote.

produce the same effect on morphogenesis as the same gene as part of the total gene complex. As however Goldschmidt's theory has already been cited by some authors in terms which suggest that it throws doubts on the whole body of theoretical genetics developed in the last twenty years, it seems advisable to add a brief note on this theory.

Goldschmidt's views are based on the well-known fact that differences in the action of the total gene complex depend not only on differences in the constituent genes, but also on differences in their arrangement in the chromosomes, as exhibited by inversions, duplications and translocations. He looks upon the whole chromosome as the unit, suggesting that it may be an immensely complex chain molecule. Mutations, he considers, are due to breaks in the links which join the sub-molecules (residues), and subsequent rearrangements of these. Although Goldschmidt considers that the classical conception of the gene would be rendered obsolete if this theory were accepted, it does not appear to involve any important revision of usually accepted views as to the nature and mode of action of the genes.³ The theory constitutes, if true, an advance, but not a revolution, in our ideas of the gene. In Goldschmidt's theory the chromosomes are still composed of locally differentiated parts, whether we call them genes or not. All the superstructure built on Mendel's experiments still depends upon the composition of the chromosomes of these differentiated parts, separable from one another and interchangeable with corresponding parts of homologous chromosomes.

Goldschmidt says (p. 311) 'the facts of genetics may, of course, be described in terms of genes, but a theory of the germ plasm would have to do away completely with the concept of the genes as units.' The fact that the total action of the gene complex depends not only on the composition of the individual genes, but also on their mutual spatial relations, is however fully compatible with the notion of the genes as units in the same sense as atoms are units of chemical action, or cells are morphological and functional units of the body. It is even compatible with the theory that the genes are elementary living organisms, in principle capable of maintaining their lives in independence of each other, as are the cells of the body.

So far we have spoken of genes as the sources of evolutionary

3. See also Waddington (1939), p. 376.

change, by gene mutations, recombinations, and rearrangements. Equally important, however, is their function of ensuring some degree of stability of the new phenotypes so produced. Evolution cannot proceed without variation, but neither can it proceed without the inheritance of such variations. Evolution demands a stability of the new forms, but also demands that the stability shall not be complete. This stability is ensured by the fact that at the beginning of each life cycle the organism contains within itself, transmitted to it by its parents, the factors (genes) which will give the process of embryonic development the same trend as it had in the parents. A mechanism of heredity became necessary, as we have pointed out, when organisms got beyond the stage of complexity when they could divide into two organisms which reconstituted themselves into systems identical with the parent organism by direct physical processes. Thus a process of embryonic development or morphogenesis such as occurs in all but the simplest organisms became necessary. The problem of ensuring that the comparatively undifferentiated germ should give rise to a differentiated adult of the same form as in the previous generation was solved by ensuring that the organism carries about within itself a specific internal environment, the gene complex, which does not itself participate in morphogenetic differentiation but remains unchanged (except for occasional gene mutation) from generation to generation. It is this internal environment which every cell carries about within its nucleus that ensures that the process of morphogenesis proceeds in the same way generation after generation.

3. Can natural selection of random variations account for evolution?

Everyone must accept the occurrence of random variations in the form of mutations which are not directed to the consequent modifications of the phenotype and the uses to which the modifications will be put. It follows that since hereditary differences between organisms arise in this way, the evolution from a common ancestor of a diversity of organisms adapted to a diversity of modes of life must take place automatically, since on the whole those organisms better able to cope with their environment will more often survive to leave descendants than those less able to do so. The problem is not whether natural selection of random variations would account for evolution of any kind whatever,

or even for the evolution of organisms with specific adaptations to specific environments, but whether it would account for the evolution of the world of organisms which actually exists. It is held by many that the adaptations, both of structure and processes, exhibited by organisms, at least by the higher organisms, are so complex that although their evolution may be formally explainable on these lines, such an explanation demands a synchronous or serially ordered multitude of mutually appropriate variations so huge as to be inadmissible as a practical hypothesis.

There is no denying that this is a formidable difficulty for this theory of evolution; on the other hand, it is impossible to form any but very uncertain judgments as to its real force. An assessment of the probability of such an orderly coincidence and sequence of variations depends partly upon estimates of the frequency of gene mutations, or of other sources of inheritable changes (if there are any), and of the number of individuals and generations which have been subjected to natural selection during the course of evolution. We know very little about these things, though it is estimated that in *Drosophila* under laboratory conditions something of the order of two per cent. of gametes carry a mutated gene. The great majority of these however do not produce any directly visible phenotypic effect in the fly and can only be revealed by further breeding. The total number of different genes in *Drosophila* has been estimated, by various means, as a few thousands. As regards the mutation rate of individual genes, this has been found in a plant (maize) to range from about five hundred to about one in a million for the half-dozen genes investigated.

More important, however, is an understanding of the effect on morphogenesis of simple variations in the initial constitution of the germ cells. Mistaken ideas about this have often led to great exaggeration of the difficulties in the theory of evolution by natural selection of random variations. This is apparent in the analogies sometimes put forward in support of their arguments by critics of the theory of evolution by natural selection of random variations. It is asserted, for instance, that to account for evolution in this way is comparable to saying that if one mixed a million letters in a bag and drew them out at random, they might spell one of Shakespeare's plays. Such analogies assume that a complex organism is a collection of parts, one added to the other, and implies that the production of the complex presents a problem in

probability of the same kind as that of the probability of a hundred successive tosses of a penny all giving heads, or of a series of letters drawn at random forming a sequence which spells out a meaningful sentence or piece of literature. But a gene mutation does not merely add or subtract a part or characteristic of the organism, nor does a new combination of genes correspond merely to a new collection of parts in the phenotype.

Although not at present referable to gene action, the remarkable and complex differences that may result from simple initial difference of protoplasms are of importance here. This has been vividly presented by D'Arcy Thompson in his well-known book, *Growth and Form*. He shows how, for instance, the most complex form of Radiolarian shells or sponge spicules develop according to the physical principles of surface tension, adsorption, and the like, from simple antecedent physical and chemical conditions in the protoplasm. The importance of this is that we do not have to account for the building up of the more complex from the simpler structures step by step, by additions here and subtractions there. A comparatively simple change in the internal physical conditions will produce the difference between a Radiolarian skeleton consisting of a few isolated rods of silica, and the beautiful and complex skeletons consisting of concentric lattice work spheres.

Thompson also shows how complex differences in the proportions of all parts of the body in different species can be reduced to differences of growth rates pervading the organism as a whole, and expressible in simple mathematical terms. Out of the wealth of material he presents, I shall select only one, the relation between the forms of the skull of the baboon, the chimpanzee and man. In a general way, these skulls are characterized by a progressive enlargement of the brain case and diminution of the jaws. Thompson shows an outline of a human skull projected on a system of a Cartesian co-ordinates consisting of a rectangle divided into squares by equidistant vertical and horizontal lines. If, on a similar projection of a chimpanzee's skull, lines are drawn through the points on the skull corresponding to those lying on the rectangular cross lines dividing the human skull, the straight lines are replaced by curves, and the areas enclosed between the intersecting curves increase in an approximately logarithmic order as we pass from above downwards and from behind forwards. A projection of the baboon's skull shows a similar but more pronounced deformation of the rectangular co-ordinates of the human

skull. Or if preferred, we can follow the inverse order beginning with the baboon's skull in rectangular co-ordinates and follow out its transformation into curvilinear and logarithmically spaced co-ordinates in the human skull.

The lesson of this is that we do not have to account for the transformation of the monkey's skull into the ape's, and the ape's into the man's, by simultaneous or consecutive selection of a large number of variations of different parts of the skull. For instance, it is unnecessary to explain the weakening of the human jaw which has accompanied the enlargement of his brain as the result of a mode of life in which intelligence rather than powerful teeth was the means of defence. A simple change in the system of forces to which the growing organism was exposed will account for both the increase in the brain case and the decrease in the jaws as well as for a multitude of other conformable changes. It is true, nevertheless, that a huge number of separate variations must have taken place in producing man and the chimpanzee from their common ancestor. But there is every reason to believe that the number is not so great as the methods of the comparative anatomist suggest.

Similarly, the diversity of responses of cells or other living agents in the general conditions of the morphogenetic fields have not to be accounted for in all their details by correspondingly detailed diversity in the fields or responding agents.

As discussed in chapter v, the genes may be considered either as supplying the internal conditions which influence the responses which embryonic cells make to given morphogenetic stimuli, or else as influencing the specificity of the stimuli themselves; indeed, they probably do both. An embryonic cell which is part of an embryo whose cells contain a certain gene complex may receive morphogenetic stimuli different from those received by a cell which is part of an embryo with a different gene complex; or to a cell with one gene complex a given stimulus means one kind of response, to a cell with another gene complex the same stimulus means a different kind of response, a different degree of response, or perhaps no response at all, just as the organism as a whole responds differently to sensa of external origin when it is in different physiological states.

Variations of stimulus or of internal states merely modify behaviour, however; the behaviour is still directed to a goal, though

the means of attaining it, or the goal itself, may be modified. A variation of the gene complex does not add nor subtract an item of morphogenetic behaviour, but modifies the previous morphogenetic behaviour. An animal in an unfamiliar situation, such as Thorndike's cats in their puzzle boxes, does not behave in a merely hysterical or unco-ordinated way. Its response to the situation is behaviour directed to a goal, not a mere sequence of muscular contractions. Similarly, the behaviour of embryonic cells with a gene complex different from that of the parent organism is not unco-ordinated or mechanical, but is a modification of the behaviour under the old conditions, directed to a modified goal or by a different route to the old goal.

Thus embryonic development has a historical character, which has given rise to the theory of recapitulation. This term implies that embryonic stages represent, in a modified form, adult stages of remote ancestors; it implies that the embryonic development of an animal is an abbreviated and modified recapitulation of its evolutionary history. I do not intend to add to the many discussions about the value of embryology as an indication of ancestral adult structure. On the view, however, that embryonic development is a complex of instinctive behaviours, its historical aspect is an expression of the fact that the course of this instinctive behaviour in the ancestors whose features are said to be recapitulated has been modified, but still displays recognizable similarities. The general features which the embryonic development of reptiles, birds and mammals have in common, such as the development of gill slits, and the structure of the heart and main blood vessels at that stage, must be considered to be still recognizable modifications of the embryonic processes of their common ancestor, which the fossil record shows must have been a fish. Thus it comes about that there is a certain degree of recapitulation of evolutionary history in embryonic development, since many of the organs of the more highly evolved forms develop by indirect routes, starting their development as if they were going to become organs of the type found in adult ancestral forms but deviating from this route as development proceeds.

As already pointed out, the case of plant galls shows what extreme but orderly modifications of the normal process of morphogenesis can be produced by a simple difference in the conditions, or the stimuli, under which the process takes place. The presence of what is probably a chemical substance, and in any case is a

specific alteration of the ordinary condition of the plant cells and tissues caused by the presence of a foreign organism, results in the formation of these highly specific structures, which are never produced by the plant in the absence of this extraneous stimulus. If, instead of being produced by a gall-fly, this stimulus was produced by a microscopic organism which entered into symbiosis with the plant, living and reproducing in a chromosome, the plant would then carry about within itself the source of the morphogenetic stimulus, and that specific type of gall would become one of the hereditary characteristics of the plant, developing in the same way as its leaves and flowers.

The great significance of the formation of such structures as plant galls lies in the fact that here there can be no question of a long process of evolution adapting the plant to make this highly specific and complex response to the stimulus provided by the gall-fly, since the galls are of no survival value to the plant. It is an example of the immense range of potential morphogenetic responses possessed by organisms but normally not evoked owing to lack of the necessary stimulus or conditions. It also illustrates what far-reaching consequences might result from a single gene mutation, and shows that the morphogenetic processes do not change in an unco-ordinated way, but so as to result in a formed structure and not a mere mass of unorganized tissue.

The action of the gall-fly can be paralleled by many experimental means of altering the normal process of embryonic development in animals, and again we find that unless the modifications of the morphogenetic process thus caused are so extreme that a viable embryo cannot result, orderly modifications of normal structures are produced. An example of this is afforded by Stockard's investigations of the effect of various depressants on the development of the eye. If small quantities of alcohol or magnesium chloride are added to the sea water in which fish eggs are developing, the two eye rudiments tend to fuse into one, giving in extreme cases a single median eye with scarcely an indication of a double origin. Here again it can be seen that a single gene mutation which resulted in the production of such depressant substances would produce in one evolutionary step an organism with a single median eye instead of the paired lateral eyes. And, in fact, many single gene mutations do affect practically the whole constitution of the organism. Many gene mutations in *Drosophila* are of this type. In man, the rare condition known as brachydactyly is shown by

its mode of inheritance to differ from the normal in regard to a single gene only. The condition takes its name from the structure of the digits. All the fingers and toes have two joints instead of three. But the bodily structure as a whole is also affected, as exemplified for instance by the short stature of brachydactylous persons.

Thus the nature of the effect on morphogenesis of gene mutations and combinations, which are undoubtedly random in the sense discussed above, certainly diminishes the force of criticisms of the theory of evolution by natural selection of random variations based upon a view of that process which finds an analogy in the production of meaningful literature by random selection of letters.

It is true that only in a small minority of cases can such modified processes of morphogenesis result in an organism better adapted to cope with its environment, in spite of the fact that they result in an orderly production of a new type of organization and not merely random additions, subtractions, or alterations of parts. But the theory of natural selection of random variations can accommodate this. It allows for the enormous majority of variations being unfavourable or neutral. Only a minute proportion of the organisms of bygone ages have become the ancestors of the animals and plants alive at the present time. Moreover, there has not been merely a selection of forms best adapted to their environments. There has undoubtedly been a selection of environments by the organisms. An animal or a plant with a modified organ which might not in any way make it better adapted to its ancestral environment, may thereby be enabled to occupy a new environment, the possibilities of which are not already exhausted by its present inhabitants. In taking account of the probability of favourable variations we have therefore not merely to reckon the chances of a variation better fitting the organism for its present environment, but better fitting it for any one of a large number of environments open to it.

Nevertheless, the coincidence and correct sequence of the variations necessary to produce the more complex organisms out of the simpler ones remain a real difficulty, though one the force of which it is difficult to assess. It should be pointed out, however, that even if it is held that random variation as at present conceived cannot provide the material for evolutionary change of the type that we believe to have taken place, it is not necessary to accept

one of the alternative or supplementary theories of evolution which have been put forward—for instance, Lamarckian inheritance, or some directing agency guiding the course of evolution to a distant goal. There may well be some factor operating in evolution no more suspected at present than in pre-Newtonian days gravitation was suspected as providing an explanation of the paths of the planets.

4. *Lamarckian inheritance*

It must be with some distaste that a biologist approaches the controversy over the Lamarckian factor in evolution, the 'inheritance of acquired characters.' Some discussion of it is necessary however, since, in disagreement with the views here maintained, many biologists, psychologists and philosophers who have adopted a psychobiological interpretation of vital processes have regarded it as affording a basis for Lamarckian inheritance and so providing a rational explanation of evolution; the dynamic factor in evolution is conceived by them as inherited experience.

The history of this controversy during the last fifty years is not one of which biologists can be proud. Histories of biological science written a century hence will surely depict it as a discreditable episode in the development of the science. Confused reasoning, misunderstanding of the problem involved, and bad experimentation, have all contributed to this situation. The term 'acquired characters' has itself added to the confusion. As has often been pointed out, this phrase is meaningless except in the special and arbitrary sense in which it is used in this connection. We cannot study the inheritance of 'characters,' but only of differences of characters. Substituting the word 'difference,' the phrase 'acquired differences' is inoffensive if it is understood that 'acquired' means acquired during the lifetime of the organism. An acquired difference is a difference between two phenotypes of identical genotype; the zygotes started with identical potentialities of development, but the phenotypes are different owing to these potentialities having been actualized in different environments. An innate, as contrasted with an acquired, difference is a difference due to different constitution of the zygotes; that is to say, of genotype. According to the Lamarckian theory, acquired differences become transformed into innate differences. The use of the expression 'acquired characters' has, however, become so ingrained in biological literature that we

shall continue to use it here, having defined its special meaning in this connection.

I do not intend to add here to the innumerable discussions as to whether Lamarckian inheritance is a fact. It is well known that the great majority of geneticists consider that the evidence for its occurrence falls very far short of what would be required to justify taking it into account in constructing our theoretical schemes of genetics, or to allow the use of it as an explanatory factor in evolution. It is, indeed, impossible not to be impressed by the fact that after fifty years of search for experimental evidence of the inheritance of an acquired character, there is still no experiment which has been established in the usual way by repetition and confirmation by other workers. Almost every experimentalist on the subject seeks for some new evidence; if his experiment appears to furnish positive evidence, it is quoted for a few years; then, in consequence of criticism, either of the experimental procedure or of the interpretation of the results of the experiment, or of the failure of other workers to obtain these results, the experiment drops from the literature and some more recent supposed evidence takes its place for a few years. Damaging comparison with the history of experiments on which real advances in science have been founded is inevitable. Nevertheless, opinion on the value of the existing experimental evidence is not unanimous, and in spite of past experience, the confirmable experiment may yet be forthcoming. Moreover, arguments for the inheritance of acquired characters based on other than experimental evidence have some force. In the discussion which follows we will therefore confine ourselves to the questions of how far the Lamarckian factor would be useful as an explanatory principle in evolution, assuming that it occurs. This, also, has been so often and so fully discussed that it can be dealt with very briefly, and only in its special reference to the thesis of this book.⁴

The theory of Lamarckian inheritance, or the theory of the inheritance of acquired characters, states that when an organism develops some characteristic, whether anatomical, physiological or psychological, in response to the action upon it of some feature of its environment (including in this its relation to other organisms, its food and so forth), its offspring tend to develop the same characteristic even in the absence of the environmental feature

4. For a discussion of the value for evolutionary theory both of the Lamarckian and Darwinian principles the reader may be referred to Sumner, and for the limitations of the former in the special sphere of the evolution of instinct, to Holmes.

which was necessary to evoke it in the parent; or expressed in another way, continued exposure of successive generations to that environment makes the response more and more pronounced. As applied to behaviour, animals learn by experience during their lifetime how to deal with the situations they encounter in their environment; according to the Lamarckian theory their offspring will in consequence be born with a greater capacity for dealing with that situation. They have inherited the knowledge or skill which their parents had to acquire by their own efforts. Or to take a physiological example, the pigment in the human skin increases on exposure to strong sunlight—undoubtedly a protective response. According to this theory, the mere fact that the parent made this response to sunlight—or, at any rate, by living in a sunny climate made it to an unusual degree—will cause his offspring to have more pigment in their skins than they would have had if the pigment-forming response had not been evoked in the parent. Thus, white men living in the tropics will in the course of generations become black by this cumulative process.

To the layman, such a notion is apt to appear simple common sense. He notices that people sunburn; he notices that on the whole white people live in temperate climates and negroes in tropical climates; he is familiar with the fact that on the whole children tend to resemble their parents, and the conclusion is obvious. If the white man lives under conditions where he becomes strongly sunburnt in each generation, his children will be born darker and darker, and if this goes on 'long enough' they will become naturally black like negroes.

For evolution, the importance of the Lamarckian factor lies in its possibility of removing or reducing the necessity for postulating random or chance variation as the basis of evolutionary change. We know that the responses of animals to stimuli tend to be adaptive, and also that an animal learns by experience how to deal with situations with which it is constantly confronted. The co-ordination of muscle and nerve increases with practice, so that skilled operations, at first performed clumsily and with difficulty, become in time perfect and easy. The skin subjected to unusual pressure thickens, thus protecting the underlying tissues. If the results of these responses were even in some degree inherited, could we not utilize this power of adaptive response to their environment as a guiding factor in evolution itself? Would not the Lamarckian factor ensure that those differences between parent

and offspring which constitute evolutionary variations are, to some degree at least, not random but in the direction of making the offspring start life better adapted to the conditions under which the species is living than its parent was at birth? In this way, according to this hypothesis, the complex instincts of animals have evolved in the course of ages. A spider has innate ability to spin a web, because it has inherited the ability which generations of its ancestors had to acquire by effort. Babies are born with thick skin on the soles of their feet because the skin there has thickened in response to pressure over many generations of ancestors.

This escape from the randomness of those variations from which adaptive characters evolve is undoubtedly attractive, but closer consideration shows that its value in this direction would be small (always assuming that Lamarckian inheritance does in fact occur). Let us consider this in the case of the evolution of specific forms of instinctive behaviour. Because, no doubt, of the observed fact that animals are capable of learning to adapt their behaviour to special conditions, the Lamarckian principle has been held to be particularly applicable here. It is indeed a fact established by many experiments that animals low down in the scale of organization—probably even the Protozoa—display some powers of learning by experience in experimental situations, and it is a fair inference that this power is much greater in the types of situation which they meet with in nature, and which are therefore more in accord with their natural modes of life. But how is this learning accomplished? It is accomplished by the process of trial and error. Unsuccessful responses are omitted, and successful responses repeated, on subsequent occasions. Successful responses are those which attain the goal towards which the animal is striving; they are responses which give satisfaction. We may probably take it as a universal property of living organisms that actions leading directly to physiological well-being are satisfying. Thus we may take it that animals do, during their lifetime, become more skilled in such actions as lead to immediate satisfaction of hunger, escape from pain, and so forth. But the satisfaction must plainly be of a direct kind, and to the actual performer of the action. In no way could the general tendency of animals to find satisfaction in actions which lead to their immediate well-being be used to explain their improving by practice in actions which conduce to the well-being, not of themselves, but, for example, of their offspring. It is impossible, for instance, to use this explanation for the evolution

of the train of actions involved in the wasp's instinctive action of constructing a nest and provisioning it with paralysed spiders which are to serve as food for its offspring, without postulating a prior psychological variation which caused the wasp to find satisfaction in constructing and provisioning nests. Given this prior psychological peculiarity, it is conceivable that each wasp might improve its skill during its lifetime and so transmit an improved skilfulness to its offspring. In short, the Lamarckian factor can only be used to explain how animals become more skilful in attaining their hormic goals. It cannot explain how animals have come to have hormic goals which lead to useful rather than to useless or harmful remote biological consequences. The fact that it is characteristic of living organisms to respond to stimuli, not only in ways which lead to their own immediate well-being, but also in ways which result in the conservation of the species, cannot be ascribed to the Lamarckian factor. Thus the sphere of utility of this factor as a factor explanatory of the course of evolution is drastically limited.

Where learning, in the true sense of discovery by trial which of a number of different actions gives satisfying results, is excluded, the value of the Lamarckian factor is still further restricted. It is very important here to maintain the distinction between true learning by experience and facilitation which has been stressed above. Learning which results in more effective ways of dealing with a situation, which is the only kind of learning relevant to evolution by Lamarckian inheritance, must involve discovery by trial of those variations of behaviour that are most successful.

Even in the sphere most favourable for the application of the Lamarckian factor, that of instinctive behaviour, examples where discovery by trial of the best form of response is excluded are innumerable; for instance, the complex process of cocoon formation by the larvae of certain Lepidoptera, in which provision is made for the eventual emergence of the perfect insect. Here there is no possibility of profiting by experience, for the insect does it only once in its lifetime and can have no experience of the consequences of doing it in different ways.⁵ Consequently 'inherited habit' would merely result in the insect tending to spin its cocoon in the way its less remote ancestors did, whether this was more or less effective than the methods employed by its more remote ancestors.

5. Unless indeed the memory factor in Lamarckian inheritance is supposed to be able to envisage the act of cocoon spinning for a series of antecedent generations and judge which was the most successful. It seems unnecessary to discuss this hypothesis.

Although we have been using the term 'Lamarckian' in a technical rather than a historical sense, it is proper to recall how Lamarck himself conceived the relation of this principle to evolution. The definition given on p. 189 expresses, I think, the meaning with which the term is used in modern biology, synonymously with the phrase 'inheritance of acquired characters.' Lamarck himself recognized the necessity of accounting for the origin of new instincts or habits, with their accompanying anatomical instruments, as well as for their perfection by use. He says (quoting from the translation by Elliott): 'But great alterations in the environment of animals lead to great alterations in their needs, and these alterations in their needs necessarily lead to others in their activities. Now if the new needs become permanent, the animals then adopt new habits which last as long as the needs that evoked them' (p. 107). As to the influence of these habits on structure, he says (p. 112): 'Every new need, necessitating new activities for its satisfaction, requires the animal either to make more frequent use of some of its parts which it previously used less, and thus greatly to develop and enlarge them; or else to make use of entirely new parts, to which the needs have imperceptibly given birth by efforts of inner feeling.'

As his examples show, when he speaks of needs, Lamarck means the kind of needs which involve hormic goals. The problem of how animals have come to feel needs, the satisfaction of which have biological consequences not striven for by the animal itself but which are necessary for the conservation of the species, was either not formulated by Lamarck, or else is to be accounted for by a more fundamental principle of evolution. For Lamarck did not hold the evolutionary factor which is always associated with his name to be the primary principle involved in evolutionary change. His primary principle was an inherent tendency to evolve from simplicity to complexity. This tendency is modified, or deflected from its natural course, by the modifications caused by inherited habits evoked by new needs which have themselves been evoked by changed environment. 'Progress in complexity of organization exhibits anomalies here and there in the general series of animals due to the influence of environment and of acquired habit.' (p. 70). By complexity of organization he means complexity of anatomical organization.

However, this historical note is a digression from our argument,

since we are not concerned with Lamarck's views on the problem, but with the problem itself. Our conclusion is, that even in its most favourable sphere, the evolution of specific forms of instinctive behaviour, and even where the possibility of learning by trial the best form of action can be granted, the Lamarckian factor is limited to accounting for the evolution of greater perfection in attaining hormic goals. It cannot account for organisms directing their actions to hormic goals which have remote biological consequences such as the survival of the species. A still further limitation of the efficacy of this factor is imposed where learning during the life history of the individual is excluded, as must be the case in a very great number of forms of instinctive behaviour, and probably from all embryonic processes, where there can be no experience of the result of performing the action in different ways.

Before leaving the subject of the inheritance of acquired characters I must make clear that nothing in the above discussion is meant to imply that it is not a very important problem. Obviously, its establishment would influence greatly our fundamental conception of living organisms. It is contended, however, that as an evolutionary factor it can only be subsidiary. It does not free us from the alternatives of random variation as the fundamental basis of evolutionary change, or of some unknown factor which brings about variations in prophetic anticipation of the uses to which they will be put.

5. *Conclusion*

We have conceived living organisms as links in the causal process which is the course of nature itself. Sensa are the forms in which they experience the action of their external world upon them, and anticipations and purposes are the forms in which they experience their own agency as causes acting back upon their external world. In other words, we have conceived them as perceiving subjects, and as nexus of perceiving subjects. It might have given the thesis a more complete and satisfying philosophical form if this purposive character of living organisms could have been accepted as supplying the driving and directing force of evolution. There is such a striking analogy between the attempts to relate itself to its environment on the part of the individual organism, and the increasingly elaborate adaptation of environment which has characterised the course of evolution, that the

mind is strongly impelled to take it as something more than an analogy. It appears, however, for the reasons outlined in this chapter, that the hypothesis that by their purposive striving organisms have brought about their own evolution is untenable. At most, those organisms which purposed the best ends, and best achieved their purposes, had the best chance of surviving and leaving offspring. But if these offspring were also successful in the same way, it was because they inherited their parents' innate tendency to purpose the right things (to give appropriate meanings to their *sensa*) and their capacity to achieve their purposes; neither of these things was improved or otherwise altered in the offspring by the parents' action itself. The offspring merely owe their existence to it, and thus the opportunity to repeat their parents' successful activities.

If our general thesis is correct, biologists must accept perception as one of their ultimate data. The theory of evolution therefore does not have to account for perception itself, but it does have to show the way in which more and more complex forms of perception have developed. The theory has also to account for the fact that the perceptions of different species of animals are usually successful; that is to say, that the act of perception does usually put the percipient in its appropriate causal relation to its external world. The theory has to account for the fact, not that meanings are given to *sensa*, but that the meanings given are usually appropriate, in the sense of leading to action which deals successfully with the situation which gave rise to the *sensa*. The only theory of evolution at present acceptable on the evidence ascribes this to the natural selection of mutations and combinations of genes, which cause changes in the process of morphogenesis of the receptor and effector agents, and therefore also in the constitution of the Central Agent generated by them. In consequence, there is hereditary variation of *sensa*, and of the meanings given to them. The direct evidence for such hereditary variation is abundant. It is well known, for instance, that even after generations of captivity, rats and mice descended from trapped wild animals retain their wildness, in contrast to the behaviour of the tame strains of rats and mice maintained for laboratory purposes all over the world, and familiar to many of us from school-boy days. Several experimental studies of the inheritance of degrees of tameness and wildness in these animals have been made. As an example we may mention an experiment by Dawson.

In order to obtain an objective measure of their wildness, the mice were placed (one at a time) at one end of a trough or runway, and the time taken by them to travel to the other end of it (a distance of twenty-two feet) was measured. The descendants of trapped wild mice, even after generations of captivity, evidently perceive this situation with the affective tone of fear, running quickly down the runway, while the tame mice proceed along it in leisurely fashion, frequently requiring prods from behind to keep them moving. The average time taken for 47 wild mice to traverse the distance was 5 seconds, and for 54 tame mice, 25 seconds. The quickest mice of the wild strain took 3 seconds, and of the tame strain, 9 seconds; the slowest mice of the two strains took 13 and 66 seconds respectively. The times taken by the second generation of descendants from crosses between tame and wild strains showed the usual evidence of segregation where several genes contribute to a phenotypic difference. The times taken by 190 such mice ranged from 4 to 53 seconds. These crosses showed also that the different behaviours of the wild and tame mice cannot be ascribed to the association of the young with the parents, for in reciprocal crosses between the two strains (in which the male parent was removed before the birth of the young, or one or two days after) the performance of the offspring was similar.

This experiment therefore shows that there is an inheritable difference in the way in which the situation of finding itself in an open space without cover is perceived by wild and tame mice, and the conclusion to be drawn from the segregation of behaviours in the second generation from the cross between wild and tame is that this inheritable difference is referable to gene differences. Many corroborative experiments and observations on animals could be quoted. The illusions and other psychic abnormalities characteristic of certain forms of hereditary insanity in man are another example. These psychoses serve to remind us that the normal man's outlook on the world, his interpretation of what reaches him from that world through his senses, and his emotional reactions, are by no means the only possible ones. Gene mutations may alter the process of morphogenesis in ways which will result (with or without the co-operation of special environmental conditions) in the most fantastic minds—fantastic, that is to say, in their divorce from reality as judged by the success or failure of their actions. It is natural selection that has brought about the

correspondence between perception and reality, as judged by the success of the resulting behaviour.

In evolution, those meanings of *sensa* which led to appropriate action secured the survival of the individual and of the race, while the others were eliminated. It is however not easy to trace, even in imagination, the detailed course of the evolution of the higher out of the lower types of perception. Whatever theory of evolution be accepted, it must start with a primitive type of organism, for which the meanings of its *sensa* were presumably a mere generalized acceptance or rejection, seeking or avoiding. This has evolved by stages into such an organism as, for instance, a wasp with its capacity of responding to a nexus of *sensa*, of internal origin from the ovaries and of external origin through the eye, by the action of constructing a nest and provisioning it with paralysed spiders. The steps in this evolution are difficult to picture, especially when we remember the long course of embryonic development which is necessary in each individual life history before this complex perception becomes possible. The problem of their evolution is, however, separable from the problem of the nature of organisms as perceiving subjects and nexus of perceiving subjects, just as the elucidation of physiological processes is separable from any theory of how these have evolved from simpler beginnings. Fortunately the study of living organisms as they are does not have to wait upon an entirely satisfactory theory of how they have come to be what they are.

REFERENCES

The titles of two journals to which many references are made are abbreviated as follows:

P.R.S.—*Proceedings of the Royal Society of London, Series B.*
A.E.M.—*Archiv für Entwicklungsmechanik der Organismen.*

Adams, D. K. 'Experimental studies of adaptive behaviour in cats.' *Comparative Psychology Monographs* 6(1). Baltimore, 1929.

Agar, W. E. 'Trial and error and intelligence in the behaviour of certain Arthropods.' *Australian Journal of Experimental Biology and Medical Science*, 11, 1925.

Agar, W. E. 'The regulation of behaviour in water-mites and some other Arthropods.' *Journal of Comparative Psychology* 7, 1927.

Agar, W. E. 'The concept of purpose in biology.' *Quarterly Review of Biology* 13, 1938.

Allen, A. H. B. *Pleasure and Instinct.* London, 1930.

Bowman, A. A. *A Sacramental Universe.* Princeton, 1939.

Broad, C. D. *Scientific Thought.* London, 1923.

Brown, G., and Sherrington, C. S. 'Note on the function of the cortex cerebri.' *Journal of Physiology* 46, 1913.

Burr, H. S., and Northrop, F. S. C. 'The electro-dynamic theory of life.' *Quarterly Review of Biology* 10, 1935.

Cannon, W. B. *Bodily Changes in Pain, Hunger, Fear and Rage.* New York, 2nd ed., 1929.

Child, C. M. *The Origin and Development of the Nervous System.* Chicago, 1921.

Child, C. M. *Physiological Foundations of Behaviour.* New York, 1924.

Clark, A. M. 'Some effects of removing the nucleus from Amoeba.' *Australian Journal of Experimental Biology and Medical Science* 20, 1942.

Dawson, W. M. 'Inheritance of wildness and tameness in mice.' *Genetics* 17, 1932.

Dingle, H. 'The philosophical viewpoint of a scientist.' *Aristotelian Society Proceedings* 39, 1938-9.

Dingle, H. A. 'A current misconception of science.' *Hibbert Journal* 38, 1939-40.

Dodge, R. 'An experimental study of visual fixation.' *The Psychological Review, Monograph Supplements*, 18, 1907.

Dragonirov, N. 'Über Koordination der Teilprozesse in der embryonalen Morphogenese des Augenbechers.' *A.E.-M.* 129, 1933.

Emmet, D. M. *Whitehead's Philosophy of Organism.* London, 1932.

Goldschmidt, R. *Physiological Genetics.* London, 1938.

Gurwitsch, A. *Die Histologischen Grundlagen der Biologie.* Jena, 1930.

Haffner, K. von. 'Die überzähligen Bildungen des Körperstammes von *Lumbriculus variegatus.*' *A.E.-M.* 123, 1931.

Haldane, J. S. *The Sciences and Philosophy.* Gifford Lectures, London, 1927-8.

Harrison, R. G. 'Correlation in the development and growth of the eye studied by means of heteroplastic transplantation.' *A.E.-M.* 120, 1929.

Hartshorne, C. *The Philosophy and Psychology of Sensation.* Chicago, 1934.

Hegner, R. W. 'The origin and early history of the germ-cells in some Chrysomelid beetles.' *Journal of Morphology* 20, 1909.

Hogben, L. *The Nature of Living Matter.* London, 1930.

Holmes, S. J. *The Evolution of Animal Intelligence.* New York, 1911.

Holzfreter, J. 'Studien zur Ermittlung der Gestaltungsfaktoren in der Organentwicklung der Amphibien.' *A.E.-M.* 139, 1939.

Hörstadius, S. 'Über die Determination des Keimes bei Echinodermen.' *Acta Zoologica* 9, 1928.

Humphrey, G. *The Nature of Learning.* London, 1933.

Huxley, J. S. 'Some phenomena of regeneration in *Sycon.*' *Philosophical Transactions of the Royal Society of London, Series B*, 202, 1911.

Huxley, J. S., and de Beer, G. R. *The Elements of Experimental Embryology.* Cambridge, 1934.

Jennings, H. S. *Behaviour of the Lower Organisms.* New York, 1906.

Kepner, W. A., and Taliaferro, W. H. 'Reactions of *Amoeba proteus* to food.' *Biological Bulletin* 24, 1918.

Köhler, W. *Gestalt Psychology.* London, 1930.

Koffka, K. *Principles of Gestalt Psychology.* London, 1935.

Kuhl, W. 'Untersuchungen über das Verhalten künstlich getrennter Furchungszellen und Zellaggregate einiger Amphibienarten mit Hilfe des Zeitrafferfilmes.' *A.E.-M.* 136, 1937.

Küster, E. *Die Gallen der Pflanzen.* Leipzig, 1911.

Lamarck, J. B. *Zoological Philosophy.* Translation by H. Elliot. London, 1914.

Lashley, K. S. *Brain Mechanisms and Intelligence*. Chicago, 1929.

Laurens, H., and Williams, J. W. 'Photomechanical changes in the retina of normal and transplanted eyes of *Amblystoma* larvae.' *Journal of Experimental Zoology* 23, 1917.

Loeb, J. *Forced Movements, Tropisms, and Animal Conduct*. Philadelphia, 1918.

Mangold, O. 'Das Determinationsproblem, III. Das Wirbeltierauge in der Entwicklung und Regeneration.' *Ergebnisse der Biologie* 7, 1931.

Mast, S. O. 'Structure, movement, locomotion and stimulation in Amoeba.' *Journal of Morphology* 41, 1926.

Mast, S. O. 'Locomotion in *Amoeba proteus*.' *Protoplasma* 14, 1931.

Mast, S. O. 'Localized stimulation, transmission of impulses, and the nature of response in Amoeba.' *Physiological Zoology* 5, 1932.

Mast, S. O. 'Factors involved in the orientation of lower organisms in light.' *Biological Reviews of the Cambridge Philosophical Society* 13, 1938.

Mast, S. O., and Hahnert, W. F. 'Feeding, digestion and starvation in *Amoeba proteus*.' *Physiological Zoology* 8, 1935.

Mast, S. O., and Pusch, L. C. 'Modification of responses in Amoeba.' *Biological Bulletin* 46, 1924.

Matthews, L. H. 'Visual stimulation and ovulation in pigeons.' *P.R.S.* 126, 1939.

McDougall, K. D., and McDougall, W. 'Insight and foresight in various animals—monkey, racoon, rat and wasp.' *Journal of Comparative Psychology* 11, 1931.

McDougall, W. *Outline of Psychology*. London, 1923.

Mott, F. W., and Sherrington, C. S. 'Experiments upon the influence of sensory nerves upon movement and nutrition of the limbs.' *P.R.S.* 57, 1895.

Needham, J. 'Neo-mechanism.' *Hibbert Journal* 25, 1926-7.

Pattel, M. D. 'The physiology of the formation of "pigeon's milk."' *Physiological Zoology* 9, 1936.

Pavlov, I. P. *Conditioned Reflexes*. Oxford, 1927.

Pavlov, I. P. 'Certain problems in the physiology of the cerebral hemispheres' (Croonian lecture). *P.R.S.* 103, 1928.

Peckham, G. W. and E. G. 'Some observations on the mental processes of spiders.' *Journal of Morphology* 1, 1887.

Peckham, G. W. and E. G. *Wasps Social and Solitary*. London, 1905.

Petermann, B. *The Gestalt Theory and the Problem of Configuration*. London, 1932.

Price, H. H. *Perception*. London, 1932.

Russell, B. *The Analysis of Matter*. London, 1927.

Schaeffer, A. A. *Ameboid Movement*. Princeton, 1920.

Sherrington, C. S. *The Integrative Action of the Nervous System*. New Haven, 1920.

Spemann, H. 'Die Entwicklung seitlicher und dorso-ventraler Keimhälften bei verzögerter Keimversorgung.' *Zeitschrift für wissenschaftliche Zoologie* 132, 1928.

Spemann, H. *Embryonic Development and Induction*. New Haven, 1938.

Steinmann, P. 'Prospektive Analyse in Restitutionsvorgängen.' *A.E-M.* 112, 1927.

Stockard, C. R. 'The influence of alcohol and other anaesthetics on embryonic development.' *American Journal of Anatomy* 10, 1910.

Stolc, A. 'Über kernlose Individuen und kernlose Teile von Amoeba proteus.' *A.E-M.* 29, 1910.

Strangeways, T. S. P., and Fell, H. B. 'The development of the isolated early embryonic eye of the fowl when cultivated in vitro.' *P.R.S.* 100, 1926.

Sumner, F. B. 'Adaptation and the problem of "organic purposefulness."' *American Naturalist* 53, 1919.

Thompson, D'Arcy W. *On Growth and Form*. Cambridge, 1917.

Tiegs, O. W. 'A study of the neurofibril structure of the nerve cell.' *Journal of Comparative Neurology* 52, 1931.

Vernon, M. D. *Visual Perception*. Cambridge, 1937.

Wachs, H. 'Restitution des Auges nach Exstirpation von Retina und Linse bei Tritonen.' *A.E-M.* 46, 1920.

Waddington, C. H. *An Introduction to Modern Genetics*. London, 1939.

Washburn, M. F. *The Animal Mind*. New York, 1926.

Weiss, P. 'Morphodynamik.' *Abhandlungen sur theoretischen Biologie* 23, 1926.

Weiss, P. 'Morphodynamische Feldtheorien und Genetik.' *Zeitschrift für induktive Abstammungs- und Vererbungslchre. Supplementband* II, 1928.

Weiss, P. 'In vitro experiments on the factors determining the course of the outgrowing nerve fiber.' *Journal of Experimental Zoology* 68, 1934.

Weiss, P. 'Selectivity controlling the central-peripheral relations in the nervous system.' *Biological Reviews of the Cambridge Philosophical Society* 11, 1936.

Whitehead, A. N. *Science and the Modern World*. Cambridge, 1926.

Whitehead, A. N. *Process and Reality*. Cambridge, 1929.

Whitehead, A. N. *Adventures of Ideas*. Cambridge, 1933.

Whiteley, C. H. 'The causal theory of perception.' *Aristotelian Society Proceedings* 40, 1939-40.

Wolters, A. W. 'On conceptual thinking.' *British Journal of Psychology* 24, 1934.

Woodger, J. H. *Biological Principles*. London, 1929.

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